Conceptual Ecosystem Models for Long-term Ecological Monitoring in the Great Lakes Network

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Abstract: Conceptual models were constructed to describe the six major ecosystems represented in the nine National Park Service units of the Great Lakes Inventory and Monitoring Network. Stressor-based box and arrow diagrams, along with descriptive narratives, were used to convey complex linkages among biotic and abiotic ecosystem components. Natural and anthropogenic drivers, stressors, and ecosystem indicators are described in the models, and specific measures related to the attributes are included. The models assist in limiting the number of potential indicators to a subset that is particularly information rich. Monitoring these attributes will provide an indication of ecosystem and resource health that will ultimately assist park managers in making adaptive management decisions.

INTRODUCTION

The National Park Service (NPS) has instituted a program to inventory and monitor natural resources in parks across the nation. To implement this program the NPS formed 32 “Networks” of parks that share common management concerns and geography. The Great Lakes Inventory and Monitoring Network (hereafter, GLKN or the Network) is composed of nine national park units in Minnesota, Wisconsin, Michigan, and Indiana. The Network is in the process of developing its monitoring program and one of the initial steps is to identify the ecological elements and processes that should be monitored in the nine parks. The conceptual models described in this document have helped the Network select its initial set of indicators (Route 2004) and will help guide future analysis of change in park ecosystems.

Environmental systems are inherently complex, with physical, chemical, and biological elements and processes that function over a wide range of spatial and temporal scales. Monitoring trends in all elements of ecosystems is not technically, logistically, or fiscally possible. The goal of the National Park Service (NPS) Inventory and Monitoring Program is to select a few key elements that reflect the health or condition of park resources. Individual networks are charged with monitoring "Vital Signs", which are ecological indicators that provide meaningful information on select ecosystem components for park managers, who, in turn, are charged with preserving natural resources unimpaired for future generations. Achieving this goal requires a common understanding between monitoring staff and park managers in regard to the ecosystems present and the dynamics that drive the constituent elements. Conceptual models that organize information and illustrate ecosystem components and interactions are an essential tool in developing monitoring plans that meet the diversity of NPS needs.

What are Conceptual Models?

A conceptual model is a visual or narrative summary that describes the important components of an ecosystem and the linkages among those components (NPS 2003). It is, by nature, a simplification of a complex system that may be imperfectly or incompletely understood. By synthesizing current scientific understanding, field observation, and professional judgment concerning an ecological system into a conceptual model, it is possible to make reasonable judgments regarding system components.

Models can be more or less complex depending on the type of model constructed and the needs of the modeler. Overly complex models are unwieldy and difficult to comprehend, limiting their utility in the planning process, while overly simplified models have inherently limited application. Considerable discussion and analysis of various model types and methods for developing monitoring programs appear in ecological literature (Maddox et al. 1999), NPS Inventory and Monitoring Program guidance documents (Gross 2003, Plumb 2003), and in Monitoring Plans of other NPS networks (NCPN 2002, SCPN 2003, GRYN 2003). Instead of reproducing that discussion here, a summary of the characteristics and usefulness of the most frequently used conceptual ecological models are summarized in Table 1.

Table 1. Comparison of common conceptual model types.

Type of model	Description	Strengths	Drawbacks
Narrative	Use word descriptions, mathematical or symbolic formula	Summarizes literature, information rich	No visual presentation of important linkages
Tabular	Table or two-dimensional array	Conveys the most information	May be difficult to comprehend amount of information
Picture models	Depict ecosystem function with plots, diagrams, or drawings	Good for portraying broad-scale patterns	Difficult to model complex ecosystems or interactions
Box and arrow (Stressor model)	Reduce ecosystems to key components and relationships	Intuitively simple, one-way flow, clear link between stressor and vital signs	No feedbacks, few or no mechanisms, not quantitative
Input/output matrix (Control model)	Box and arrow with flow (mass, energy, nutrients, etc.) between components	Quantitative, most realistic, feedback and interactions	Complicated, hard to communicate, state dynamics may not be apparent

Although conceptual models are required under the NPS guidance as one step in the development of a Vital Signs monitoring plan, the type of model used by individual networks is not stipulated (NPS 2003). The essential factor is that the conceptual models summarize the current understanding of park ecosystem attributes, processes, dynamics, and linkages (NPS 2003).

Role of Models in Monitoring Plans

The relationships between societal values protected by parks and ecological integrity must be understood by all parties (Noon 2003). Conceptual models provide the means of communicating about the myriad of components in an ecosystem and the complex interactions among the natural and anthropogenic processes in that ecosystem. Conceptual models are not ends in themselves, but rather they are a tool for organizing and illustrating knowledge of priority resources at suitable spatial and temporal scales (Maddox et al. 1999). As such, model construction must begin early in the planning process and remain a key component of monitoring plan development and implementation.

Monitoring studies must be designed to evaluate something specific, but it is seldom possible to monitor the agents that drive ecosystem change directly. Because a model describes the important biotic and abiotic linkages, it identifies those variables in the ecosystem that could be measured and relates them to the agents of change (Maddox et al. 1999, DeAngelis et al. 2003). Key attributes are then selected from the measurable variables identified in the models using predetermined criteria.

Models are based on the best available understanding of ecosystems, but they are not complete or static constructs. As information is gained through monitoring, the models will continue to be refined so that they add to our understanding of the ecosystem and our ability to monitor it effectively.

GREAT LAKES NETWORK MODELING PROCESS

Ecosystems

The GLKN staff met with the Network Technical Committee - an eleven member group of park, regional, and Network representatives - to identify the environmental components to be modeled. The Committee determined that the diverse environments found within the GLKN parks are adequately addressed through six broad conceptual models:

Earth Processes	Inland Lakes
Northern Forests	Large Rivers
Wetlands	Large Lakes

These six ecosystems are interconnected within parks and throughout surrounding areas, and as such, they share many of the same ecological pathways.

Model Format

After discussing various formats, the GLKN staff and Technical Committee decided to use a stressor based modeling approach with both a narrative and a 'box and arrow' diagram to show major pathways and linkages (Table 2). Although no feedback loops and few mechanisms are represented, we expect to develop more complex models when we focus more narrowly on specific monitoring questions in the future. Model authors were asked to identify the key ecosystem properties and processes, an essential first step in successful model construction (Maddox et al. 1999). The Network specified the elements for each level of the model diagram to ensure consistency across all models (Table 2). Further, we asked that the narrative describe major drivers, stressors, effects, and indicators through a summary of pertinent literature. Finally, we asked that modelers provide example monitoring questions and corresponding measures.

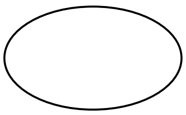
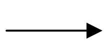
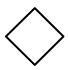
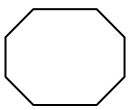
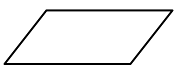
Model authors use the terms *indicator* and *Vital Sign* interchangeably, hence a brief explanation is necessary. The term *indicators* can be defined as a subset of attributes that is particularly information-rich in the sense that their values are indicative of the quality, health, or integrity of the larger ecological system. The National Park Service uses the term *Vital Signs* to describe those indicators that are important for the understanding and management of national parks. These can be physical, chemical, or biological elements and processes of natural systems that represent the overall health or condition of the system, have known or hypothesized effects of stressors, or are elements that have important human values (such as species of special concern). For the most part, the models identify potential *indicators*, using the more objective definition pertaining to ecosystem health, as opposed to *Vital Signs*, that include the more subjective human values attributes. Route (2004) discusses the Network's selection of Vital Signs in detail.

Model Authorship and Review

Model authors were selected from scientists known to GLKN or park staff (Table 3). Each author was an acknowledged expert in the subject ecosystem. Authors were given guidelines as to the type of model, definitions for key terms and symbols (Table 2), and in most cases, an example model was provided as a template.

The Network coordinated a review of draft models by at least two peers for each model (Table 3). Authors were given an opportunity to respond to review comments in subsequent revisions. The editors of this report made final judgment on differences of opinion and made certain grammatical and editorial changes to provide consistency.

Table 2. Components of the 'Box and Arrow' conceptual models used by the Great Lakes Inventory and Monitoring Network in identification of Vital Signs (adapted from NPS 2003).

Symbol	Model Component
	*Drivers* are major external driving forces such as climate, fire cycles, biological invasions, hydrologic cycles, and natural disturbance events (e.g., earthquakes, droughts, floods) that have large scale influences on natural systems.
	*Stressors* are physical, chemical, or biological perturbations to a system that are either foreign to that system or natural to the system but occurring at an excessive or deficient level. Stressors cause significant changes in the ecological components, patterns, and processes in natural systems. Examples include air pollution, water pollution, water withdrawal, pesticide use, timber and game harvest, and land-use change. They act together with drivers on ecosystem attributes.
 or 	*Ecological effects* are the physical, chemical, biological, or functional responses of ecosystem attributes to drivers and stressors.
	*Attributes** are any living or nonliving environmental feature or process that can be measured or estimated to provide insights into the state of the ecosystem.
	*Measures* are the specific variables used to quantify the condition or state of an attribute or indicator. These are specified in definitive sampling protocols. For example, stream acidity may be the indicator; pH units are the measure.

* Vital Signs are a subset of attributes that are determined to be the best indicators of condition, or respond to natural or anthropogenic stresses in a predictable or hypothesized manner, or may haves high value to the park or the public (e.g., endangered species, charismatic species, exotic species).

Table 3. Great Lakes Inventory and Monitoring Network conceptual model authors, affiliations, and number of reviewers.

Model	Authors	Affiliations	Number Reviewers
Geophysical	Walter Loope	USGS-Great Lakes Science Center *Ecologist, Munising Biological Station*	3
Inland Lakes	Paul Sager	University of Wisconsin-Green Bay *Professor Emeritus*	6
Large Lakes	Glenn Guntenspergen	USGS-Patuxent Wildlife Research Center *Ecologist*	4
Large Rivers	Ken Lubinski	USGS-Upper Midwest Environmental Sciences Center	3+
Northern Forests	Jerry Belant Phyllis Adams	NPS-Pictured Rocks National Lakeshore *Director, Pictured Rocks Science Center and Terrestrial Ecologist* NPS-Midwest Region *Inventory and Monitoring Coordinator*	3
Wetland	Joan Elias Daren Carlisle	NPS-Great Lakes Inventory and Monitoring Network *Aquatic Ecologist* USGS-National Water Quality Assessment Program *Invertebrate Ecologist, Ecological Synthesis Team*	2

+ additional internal USGS review

Summary of Major Findings

To summarize the model results, Network staff grouped the drivers and stressors identified by the authors into categories reflecting major "causes of change" (Table 4). This is consistent with the definition we provided to model authors for drivers and stressors, which "act together to cause change in ecosystems" (Table 2; see also Noon 2003). The modelers often grouped (lumped and split) drivers and stressors in different ways or they named them differently. To provide a consistent summary we used coarse groupings and a liberal interpretation of the author's terminology to capture the major causes of change. For example, neither "climate" nor "weather" was specifically named as a driver or stressor in the Earth Processes Model, yet *weathering* (referring to erosion), *wind*, and *wave action* were. These processes are influenced by climate in the long term and weather patterns in the short term. Hence we included "climate/weather" as a cause of change identified by the Earth Processes Model. We treated the other model terminology similarly. The results suggest there are 11 major causes of change in the Great Lakes Network parks with climate/weather, human development, human use, and polluted air and water influencing on all six of the major ecosystems we modeled.

Table 4. Major causes of change as identified using six conceptual models representing ecosystems of nine parks in the Great Lakes Inventory and Monitoring Network.

	Conceptual Models[1]						
Causes of change[2]	**Great Lakes**	**Inland Lakes**	**Large Rivers**	**Wetlands**	**Northern Forests**	**Earth Processes**	**No. models**
Climate and weather	X	X	X	X	X	X	6
Human development	X	X	X	X	X	X	6
Human use	X	X	X	+	X	X	6
Polluted air and water	X	X	X	X	X	+	6
Exotic and invasive species	X	X	X	X	X		5
Erosion and sedimentation	+	X	X	X		X	5
Water levels	X	+	X	X		X	5
Natural biotic processes	X	+	+	X	X		5
Habitat loss and alteration	+	+	+	+	X		5
Fire and fire suppression		X		X	X	X	4
Natural physical processes	X		X			X	3

1 = An “X” indicates that the model author(s) identified the agent of change as a driver or stressor in the model while a “+” indicates those that Network staff added for consistency.

2 = Causes of change is used here to include all drivers and stressors which act together to cause change in an ecosystem.

Causes of change can be completely natural, that is, ‘natural biotic processes’, such as predation, disease, and herbivory. They can also be anthropogenic, such as ‘human use’, including harvest and recreation. Finally, some of the major causes of change can be both natural and anthropogenic. ‘Habitat loss and alteration’, for example, includes natural forest succession along with human-induced changes.

Over 70 ecosystem attributes and more than 100 measures were identified by authors of the six models. Although differences in the naming and grouping of attributes and measures make it difficult to summarize here, the attributes and measures identified in the models, together with the monitoring issues and questions identified at meetings with the parks (Route 2004), were the raw material from which candidate Vital Signs were chosen. Thus the models were an important step in determining what the Network will monitor in the future.

Model Presentations

The complete conceptual models, including narratives and diagrams, are presented on following pages. Illustrations are numbered within each model to retain authors’ reference (i.e., each model restarts with Figure 1). Polygon shapes were edited in some diagrams, where possible, to produce consistency with the original model format among all models; a few connecting lines were consolidated for clarity. None of the authors' text was deleted or appended in the diagrams. Driver, stressor, effect, attribute and measure levels were labeled, to the degree possible, when not labeled by the author. References cited by authors are found at the end of each model.

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Upper Great Lakes Earth Processes Model

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INTRODUCTION

Geomorphic Setting of Upper Great Lakes National Parks

Six of the Upper Great Lakes National Parks lie within the Great Lakes Section of Fenneman's (1938) "Central Lowlands" geomorphic province (Indiana Dunes National Lakeshore (NL) (INDU), Sleeping Bear Dunes NL (SLBE), Pictured Rocks NL (PIRO), Apostle Islands NL (APIS), Saint Croix National Scenic Riverway (SACN), Mississippi National River and Recreation Area (MISS). Three (Isle Royale National Park (NP) (ISRO), Grand Portage National Monument (GRPO), and Voyageurs NP (VOYA)) lie within Thornbury's (1965) "Superior Upland" geomorphic province. These divisions are based on similarity in topography. Topographic expression is a function of several factors: formative tectonics, internal structure, erosional and sedimentary processes acting on the land, the intensity of processes, and the length of time such processes have been operating. These factors contribute to the understanding of the stability of natural landscapes and why one might want to monitor them.

The Central Lowlands Geomorphic Province is surrounded by higher land. Much of the province is characterized by near planar Paleozoic rock strata and by widespread glaciation (Farrand and Bell 1982, Farrand and Drexler 1985). Structures (e.g., Michigan Basin, Illinois Basins) are broad and gently dipping (Thornbury 1965). Thickness of glacial deposits in the Central Lowlands varies greatly. While the area has been glaciated and deglaciated several times within the last 2,000,000 years, the most recent (Wisconsinan) glacial episode is responsible for most of the present topography (Thornbury 1965). The Great Lakes themselves have fluctuated on a semi-periodic basis after the retreat of Wisconsin ice (Thompson and Baedke 1997, Baedke and Thompson 2000).

The Superior Upland Geomorphic Province is one of two extensions of the Laurentian Upland into the United States. It is characterized by relatively high-relief glaciated terrain and is underlain primarily by Precambrian bedrock. Rock has been folded into many ancient and complex structures.

Regolith, Potentially Mobile Earth Material

The context of monitoring geological processes or geological vital signs may be somewhat non-traditional. Questions to ask at the onset include: what are we monitoring and why? The task of monitoring implies expected change that we can perceive in and slightly beyond the human time frame. Although geological processes are notoriously variable, they are generally seen to operate at very slow rates. Bedrock configuration, geological structure, and paleontological features are examples of geological parameters that cannot be expected to change much in a human time frame. Regolith (non-bedrock, unconsolidated, mineral matter that sits atop the geologic column) is, however, often vulnerable to measurable change within the human time frame. Most monitoring issues and/or vital signs associated with geological processes will involve anticipating changes in the configuration of regolith. Studies of the movement of regolith are the province of surficial geology or geomorphology.

DRIVERS OF LANDSCAPE CHANGE

Of Thornbury's (1969) processes that shape the earth's surface (below), NPS will primarily be involved in monitoring various types of "gradation."

Epigene or Exogenetic Processes

Gradation

- A. Degradation
  - 1. Weathering
  - 2. Mass wasting or gravitative transfer
    - Rockslides, mudslides, mud-earth flows
    - Slumps
    - Soil creep
  - 3. Erosion (including transportation) by:
    - Running water
    - Groundwater
    - Coastal process: currents, longshore drift/storage
    - Wind
    - Glaciers
- B. Aggradation by:
  - 1. Running water
  - 2. Groundwater
  - 3. Coastal process: waves, currents, longshore drift/storage
  - 4. Wind
  - 5. Glaciers
- C. Work of organisms, including man

Hypogene of Endogenetic Processes

Diastrophism (e.g., folding, faulting, epirogenic uplift)
Vulcanism

Extraterrestrial Agents

Infall of meteorites

NATURAL AND ANTHROPOGENIC AGENTS OF CHANGE

Dominant Natural Drivers of Geomorphic Change

Set within the North American continental interior, environments of the nine parks in the Great Lakes Network are underlain by pre-Cambrian to Pennsylvanian age bedrock (600+ to 250 million years) (Dorr and Eschman 1970), with Paleozoic age rocks gently folded into subtle basins and domes. Most of the landscape is characterized by regolith of glacial deposits less than 15,000 years old (Thornbury 1965). Well-defined landforms, poorly integrated drainage and abundant wetlands are common (Albert et al. 1986, Keough et al. 1999).

All of the Network parks were covered with Wisconsinan glaciers and are covered with surficial glacial drift (outwash, till and related deposits) of various thicknesses. This drift has been degraded and/or rearranged naturally since the most recent glacial retreat. Upland landforms are subject to natural mass wasting (i.e., down slope movement of regolith under variable moisture conditions) as well as natural erosion (e.g., dune building and fluvial erosion). Unconsolidated sandy regolith commonly crops out in lower landscape positions along the shores of the upper Great Lakes and is regularly destabilized by natural fluctuations of Great Lakes water planes (Bishop 1990, Colman et al. 1994, Anderton and Loope 1995, Arbogast and Loope 1999, Fishser and Whitman 1999). Landscapes that are most likely to change are places where land meets water. Natural, lake-level mediated, dune dynamics generate a shifting habitat mosaic required by native plant assemblages (Olson 1958a, Olson 1958b, Olson 1958c, McEachern 1992, Maun 1998). Perched dune fields along Lakes Superior (PIRO) and Michigan (SLBE) are among the best developed in the world (Dorr and Eschman 1970). In addition to lake level fluctuation, fire also has a potential to influence dune building (Filion et al. 1991).

Along sandy portions of the Upper Great Lakes shoreline, propensity to change can differ greatly with position relative to streams of littoral sand drift and the texture of bluff substrate. The same lake level and storm surge behavior can result in bluff retreat, recession or progradation of the shore depending on location (Chrzastowski and Thompson 1992). Thus, it is important to apply the results of coastal studies in proper context.

Anthropogenic Drivers of Change

Because human use often causes unnatural disturbances in sandy landscapes, the development of a framework wherein naturally dynamic landscape processes can be distinguished from anthropogenic disturbance is required.

Visitors cause changes in the surficial landscape in many ways. For example, trampling removes vegetation and promotes gullies, breaking down of stream banks adds to sediment loads and alters natural stream aggradation/erosion, and walking on sand dunes alters natural eolian regimes. Harm to natural features and alteration of natural process often stems from on-site or adjacent construction of infrastructure. Among sand beaches, benches, and dunes of the upper Great Lakes national parks, damage most commonly results from placement of structures that protect against water erosion. Structures such as revetments, groins, and other shore armoring always alter natural processes to varying degrees and, in many cases, prove ineffective even from an engineering perspective.

ATTRIBUTES OF THE PHYSICAL SYSTEM

Remnant Coastal Features

Prominent beach ridges, spits, barriers, wave-cut terraces, deltas and dunes, now perched high above many lakeshores, represent a strong signature of prior, much higher, lake-levels. These levels were the result of a unique set of circumstances that will not be repeated in any human time frame. Thus, while shore processes continue to periodically re-create a characteristic suite of landforms, there are coastal landforms that can be thought of as 'non-repeating units'. The special circumstances of genesis of these landforms may justify higher frequency of monitoring.

Landscape Change with Lake Level Fluctuation

Natural fluctuations of Great Lakes water levels are the result of climatic variability. This variability has driven quasi-periodic (approximately 150 years) lake level change over at least the past 5000 years (Thompson and Baedke 1997, Baedke and Thompson 2000). High lake stands have been shown to influence coastal dune building and local hydrology (Anderton and Loope 1995, Loope and Arbogast 2000). Thus, the shores of many Network parks are naturally quite dynamic.

By and large, lake-level fluctuation drives changes in patch size, shape, and distribution that provides the mosaic of habitat required by several rare plant species. Thus, monitoring of physical change should be coordinated with monitoring these rare species.

Paleoecological Perspectives

Numerous paleoecological studies have shown that physical and biological characteristics of the Great Lakes Network of parks have varied significantly over millennial and centenary time frames (e.g., Booth et al. 2002). This perspective is invaluable in the development of a framework for monitoring contemporary physical process. The fact that a physical event has not occurred in human history is no proof that such an event is not crucial to the structure of the modern landscape.

EXAMPLES OF POTENTIAL MONITORING QUESTIONS

Steps in Determining Monitoring Priorities

Monitoring programs relate to both natural and anthropogenic change. In systems such as sand dunes, it is difficult to distinguish between the two. The first tool in development of a monitoring program for the surficial landscape is an understanding of natural dynamics of the broad classes of landforms in the subject park. Some landforms may be stable for thousands of years (upland bedrock plateaus); some respond to natural but infrequent events (heavy rainfall over several months; heavy precipitation or storm events) and some are naturally dynamic on an annual or lesser time frame (stream runoff regimen, beach cross-profile, and sand dune, coastal spit and rivermouth morphology).

Park Priorities in Monitoring of Geomorphic Processes

In terms of geological processes and natural physical features, the nine Network parks can be stratified into several groups with similar monitoring needs:

1) Landscapes dominated by bedrock: APIS, GRPO, ISRO, and VOYA

2) Sandy and dune landscapes: APIS (in part), PIRO, SLBE, and INDU

3) Landscapes dominated by river channels and flood plains: SACN and MISS.

While Group 1 parks are dominated by bedrock, each bedrock core has been “decorated” by surficial deposits that are particularly valuable and vulnerable. Apostle Islands NL, for example, owes its spits, bars, and tombolos to variations in levels of Lake Superior over centuries and millennia. These features cannot be expected to regenerate on decadal or shorter time scales. Thin glacial drift, plastered onto the crests of the islands, is vulnerable to erosion in instances of high human use.

Group 2 parks may be most vulnerable to alteration due to human use. For that reason, they may be of highest priority for monitoring of physical changes. Since dunes are by nature open, they are generally accessible and attractive to users who may cause severe damage. Appreciable use by even the lowest impact users can render dunes in physically altered states and lead to unnatural physical processes.

Group 3 parks represent the most robust systems in terms of short-term alteration of physical states and processes. Flooding of river corridors provides natural disturbance, the lifeblood of the system. If, however, flow regimes or sediment load are likely to be unnaturally altered over long time frames, monitoring may be of crucial importance.

METRICS OF STRESSORS

Great Lakes levels
Storm surge frequency, strength
Visitor numbers, activities

EXAMPLES OF BROAD METRICS OF GEOMORPHIC CHANGE

Rates of bluff retreat
Rates of beach recession/progradation
Stream bank stability, continuity
Stream sinuosity, downcutting
Dune building, stabilization
Stability of lake edge terraces
Stream sediment flow
Longshore sediment transport

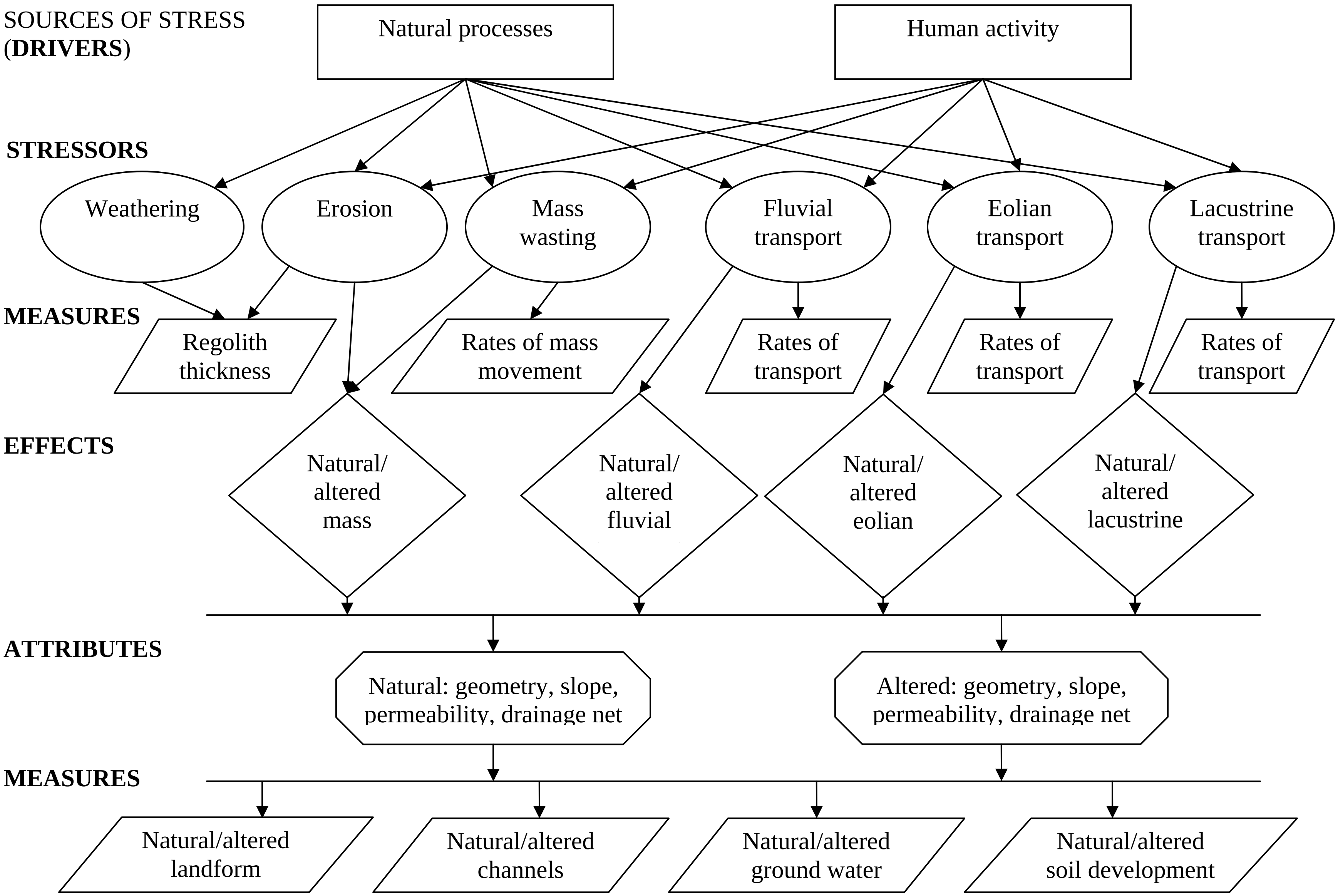

Figure 1. Conceptual physical model of the Upper Great Lakes. Model developed for the NPS Great Lakes Inventory and Monitoring Network of Parks to illustrate connections between selected attributes (Vital Signs) and system drivers.

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GREAT LAKES FORESTS CONCEPTUAL MODEL

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INTRODUCTION

For purposes of this model, we defined forests using the definition of Forest Land incorporated by the U.S. Forest Service (USFS) National Forest Health Monitoring Program (USDA USFS 1988). Forest Land is defined as:

> "*Land that is at least 10 percent stocked by forest trees of any size, or land formerly having such tree cover, and is not currently developed for a nonforest use. The minimum area for classification as forest land is one acre. Roadside, stream-side, and shelterbelt strips of timber must have a crown width at least 120 feet in width or an acre in size. Grazed woodlands, reverting fields, and pastures that are not actively maintained are included if the above qualifications are satisfied.*"

Forests overall comprise the largest single broad vegetation classification type in the Great Lakes region. In general, forests contain greater biological diversity than any other terrestrial vegetation type (Ricklefs 2001). At the time of European settlement, forests covered about half of the conterminous United States (Spies and Turner 1999). Worldwide, they are important for maintenance of biotic diversity, nutrient cycling, and consumptive and nonconsumptive human activities. Hunter (1999) describes forests and their associated diversity as having ecological, economic, educational, scientific, and spiritual values. Within the Great Lakes Network (Route and Elias 2003) there are two conifer- and five deciduous-dominated forest types (Barbour et al. 1999). Conifer forests include the boreal and Great Lakes pine forests; deciduous forests include the northern hardwoods ecotone, maple and basswood forest, beech and maple forests, oak savanna ecotone, and oak-hickory forests.

This conceptual Great Lakes forest model is stressor based and developed within a risk assessment framework. The model is an intentional simplification of forest ecosystem function. The model (Figure 1) depicts general pathways in which driving forces (rectangles) affect attributes (octagons) of the system that are intrinsically important to ecosystem function or are generally viewed by humans as valuable and/or important to maintain. Drivers are manifested as stressors (ovals) that exert effects on the ecosystem in several broad categories or 'effects' of ecosystem function (diamonds). Performance measures (rhombuses) provide broad parameters from which stressors and attributes can be measured to determine the direction and intensity of effects.

In this forest model, the three principle drivers are Human Development, Resource Extraction, and Natural Processes. They exert effects through eight principal stressors:

Pollutants and Chemical Loading
Invasive Exotics
Habitat Loss and Fragmentation
Fire and Fire Suppression
Harvest

Insects and Disease
Climate and Weather
Herbivory

Principal effects of these stressors have been grouped into five categories:

1) Ecosystem Contamination
2) Altered Watershed and Landscape
3) Altered Hydrology
4) Altered Diversity, Community Structure, and Dynamics
5) Altered Nutrient Cycle and Budget.

Ecosystem attributes are intended to provide a parsimonious subset of biological, physical, and chemical elements of the system which are representative of overall ecological conditions of the system. As with other conceptual models, most if not all of the drivers, stressors, effects, and attributes are interrelated. A major purpose of this model is to elucidate important relationships among these levels.

FOREST TYPES IN THE GREAT LAKES NETWORK

A number of definitions and classification systems have been developed for forests. Most systems developed to date have categorized vegetation into regional units based on physiognomy (e.g., alliances, cover types). Regional vegetation units are typically subdivided into categories incorporating growth form, leaf traits, and climate. For the purpose of this model, we will use the classification system described by Barbour and Billings (1998) and Barbour et al. (1999). This classification system is related to an earlier system developed by Braun (1950) which incorporates broad regional-like vegetation characteristics. We used this classification system because it incorporates dominant overstory characteristics, transition zones or ecotones, and is intuitive.

Conifer forest

Conifer forests are dominated by coniferous, or cone-bearing tree species. Gross characteristics of conifer forests include high leaf area index, relatively low diversity, shorter growing season, low net primary productivity and standing biomass, and slow litter decay and nutrient cycling. In the Great Lakes Network, two major types of conifer forests exist and are described below.

Boreal forest. - Boreal forests are circumpolar in distribution. Boreal forest is the single largest vegetation type in North America, representing about 25 percent of the landscape (Barbour et al. 1999). Common species include spruce (*Picea* spp.) and birch (*Betula* spp.). The boreal forest occurs at lower elevations and has comparatively low species diversity. This forest type is interspersed with numerous lakes, ponds, and bogs. Climate is typified by cool temperatures (annual average <5^{o} C) and short growing seasons (typically <100 days). Temperature is moderated at lower latitudes and along ocean and Great Lakes coasts. Because of low temperatures, litter decomposition is low and accumulates at ground level. Litter produces high amounts of organic acids such that soils are usually podsolized and of low fertility. In the Great Lakes Network, the boreal forest is most prevalent in Voyageurs National Park (NP), Grand Portage National Monument, and Isle Royale NP, with disjunct stands (or boreal forest components) also occurring in Apostle Islands National Lakeshore (NL) and Pictured Rocks NL.

Great Lakes Pine Forest. - Great Lakes pine forests consist of a mosaic of deciduous and conifer stands occurring in parts of Minnesota, Wisconsin, and Michigan. These forests are comprised often of nearly pure stands of near even-aged trees, predominantly red pine (*Pinus resinosa*), eastern white pine (*Pinus strobus*), or jack pine (*Pinus banksiana*). The forests often occur in sandy areas too dry to support other species. This mosaic occurs within the ecotone of the boreal and deciduous forests and is considered an edaphic climax seral stage on sites with inadequate moisture to support the hemlock-northern hardwood forest (Barbour et al. 1999). In the Great Lakes Network, pine forests are most prevalent in Saint Croix National Scenic Riverway (NSR).

Deciduous forest

Deciduous forests are forests dominated by tree species with leaves that are replaced annually. Deciduous forests occurred originally across about one-third of the conterminous United States and 10 percent of North America (Barbour et al. 1999). As compared to conifer forests, gross characteristics of deciduous forests include low leaf area index that allows greater light penetration, comparatively high species diversity, longer growing season, high net primary productivity and standing biomass, and more rapid litter decay and nutrient cycling. The dominant soil types in deciduous forests of the western Great Lakes are alfisols (gray-brown podozolics), which are moist and slightly acidic with high fertility and spodosols, also slightly acidic with a shallow leached horizon and deeper deposition layer than alfisols (Ricklefs 2001). In the Great Lakes Network, there are four major types of deciduous forests described below.

Northern Hardwoods Ecotone. - This vegetation type is also referred to as the hemlock-white pine-northern hardwood forest (Braun 1950). This ecotone is centered at 45 degrees north latitude. Dominant hardwood species includes sugar maple (*Acer saccharum*), yellow birch (*Betula allegheniensis*), beech (*Fagus grandifolia*), paper birch (*Betula papyrifera*), and basswood (*Tilia americana*). Conifer species include hemlock (*Tsuga canadensis*) and white, red, and jack pine. The northern hardwood ecotone merges to the south into beech-maple or oak-hickory forests. Within the northern hardwoods ecotone lies the Great Lakes pine forest. This forest type is most prevalent in Apostle Islands NL, Pictured Rocks NL, and Sleeping Bear Dunes NL.

Maple and Basswood Forest. - These forests occur immediately south of the northern hardwoods ecotone in Wisconsin and Minnesota and is included in Braun's (1950) hemlock-white pine-northern hardwoods. Dominant tree species are sugar maple and basswood. This vegetation type is most prevalent in Saint Croix National Scenic Riverway.

Beech and Maple Forest. - This forest type occurs immediately south of the northern hardwoods ecotone in Michigan and is dominated by beech and sugar maple. Associate species include red maple (*Acer rubrum*) and white ash (*Fraxinus americana*). This vegetation type occurs at Indiana Dunes NL and Sleeping Bear Dunes NL. A strong beech component also occurs in deciduous forests at Pictured Rocks.

Oak Savanna Ecotone. - This ecotone occurs immediately south of the maple and basswood forest in Wisconsin and Minnesota. Within this vegetation classification occurs the transition from eastern deciduous forests and grasslands. Dominant tree species include bur oak (*Quercus macrocarpa*), white oak (*Q. alba*) and several species of *Carya*. This vegetation type occurs within Saint Croix NSR and Mississippi National River and Recreation Area.

Although not within any Great Lakes Network park units, near the eastern boundary of Indiana Dunes NL lies the oak-hickory forest, dominated by several species each of *Quercus* and *Carya*. This vegetation type occurs south of the beech-maple forest.

ECOSYSTEM DRIVERS

All ecosystems are influenced by natural and anthropogenic factors. Variation in climate and associated changes in fire, succession, weather, and herbivory are important natural processes affecting forests. Through contaminant loading via atmospheric deposition, resource extraction, and other land use patterns, every forest on Earth has been affected by anthropogenic factors.

Land use patterns (e.g. human development) and resource extraction (e.g., timber harvest) are the dominant anthropogenic influences on forests. These influences occur within the context of several natural processes that also influence forest ecosystems.

For the purpose of this model, Ecosystem Drivers refer to the dominant natural and anthropogenic forces that influence forests. Each ecosystem driver causes change (i.e., stress) in the ecosystem. We defined stress as a perturbation applied to a system which is a) foreign to that system or b) natural to that system but applied at an excessive (or deficient) level. Chemical contamination and suppression of naturally-ignited fires are examples of stressors to forests. Each major ecosystem driver and its associated stressors are discussed briefly below.

Natural Processes

Important natural stressors identified are fire, insects and disease and climate/weather. Fire has a profound effect on all terrestrial ecosystems, affecting soils, hydrology, biotic communities, and nutrient availability (DeBano et al. 1998). Maintenance of several forest types requires periodic fire. Insects such as spruce budworm have had widespread effects on forest landscape patterns, community structure, and succession. Climate has a strong influence on ecosystems and is considered the major force defining boundaries of terrestrial biomes (Barbour et al. 1999). Weather can also have profound effects on forests including windthrow and precipitation patterns and events (e.g., ice damage). Larger scale weather events such as El Nino, which is associated with periodic changes in air pressure patterns over portions of the Pacific Ocean, strongly affect all terrestrial ecosystems, including forests.

Anthropogenic Processes

Important anthropogenic stressors identified for the forest model include pollutant/chemical loading, invasive exotics, habitat loss/fragmentation, harvest, and fire or fire suppression. Pollution, particularly atmospheric pollution, threatens the environment on a global scale (Barbour et al. 1999). Invasive species have altered virtually every ecosystem on earth. It has been estimated that >50,000 exotic species have been introduced to the United States alone (Ricklefs 2001). Human settlement patterns have resulted in loss and fragmentation of forests for thousands of years, leading to pronounced changes in abundance and distribution of forest communities. In northern Wisconsin, timber harvest has resulted in predominantly second growth forests in what was formerly old-growth eastern hemlock and mature northern hardwoods (White and Mladenoff 1994, Spies and Turner 1999). Human-initiated fires change surface organic materials and nutrient storage (DeBano et al. 1998). Both fire and fire suppression alter forest succession and associated community structure.

STRESSORS AND THEIR ECOLOGICAL EFFECTS

Pollutant/Chemical Loading

Pollutants and chemicals refer to any anthropogenic chemical or compound that reaches forests and could have toxic effects on organisms or larger system groupings (e.g., communities). Forests receive pollutants and chemicals from direct release, atmospheric deposition, flooding events, and through lateral transfer from aquatic systems.

Other examples of pollutants and their effects include destruction of the ozone layer through use of chlorofluorocarbons (CFCs). This has resulted in an increase in ultraviolet radiation reaching Earth which adversely affects photosynthesis in plants. Although use of CFCs has been banned in many countries, it may take a century for ozone levels to recover (Ricklefs 2001). Atmospheric concentrations of carbon dioxide have increased with burning of fuel and could increase temperatures globally 2°-6° C in the next 100 years (Barbour et al. 1999). Another example of atmospheric deposition affecting forests is acid rain, principally sulfur dioxide emissions.

Toxic chemicals, including heavy metals, can enter forests from aquatic systems through flood events in which aquatic sediments are redeposited in forests. Sulfur-based compounds enter aquatic systems through atmospheric deposition. Likely a larger factor in the Great Lakes is lateral transfer of pollutants from aquatic systems. Numerous vectors can distribute toxins across systems. Examples include emerging aquatic insects which enter the forest system, herbivory of aquatic macrophytes by moose (*Alces alces*), and removal of anadromous fish and other aquatic organisms by animals such as river otter (*Lontra canadensis*) or black bear (*Ursus americanus*) through consumption and defecation.

Non-native Invasive Plants and Animals

Thousands of plants and animals have been introduced to North America in the last 200 years (Ricklefs 2001). The effect of non-native invasive (exotic) species on forest systems has been well summarized (Barbour et al. 1999, Ricklefs 2001). Exotics plants and animals frequently alter biotic diversity, community structure, and trophic relationships through displacement of native species through competition or other means. Many invasive plant species in forests have been intentionally planted as ornamentals, biological control agents, escaped from cultivation, or have been otherwise inadvertently transported by humans. Examples of plant species that have invaded forested areas in the Great Lakes Network include garlic mustard (*Alliaria officinalis*), buckthorn (*Rhamnus* spp.), honeysuckle (*Lonicera* spp.), and *Vinca* spp. Earthworms have also been introduced throughout the northern portion of the Great Lakes Network. Earthworms have been demonstrated to alter soil conditions and modify herbaceous plant communities (Hale 2004).

Habitat Loss/Fragmentation

Habitat loss results primarily from human development (e.g., construction of homes, industry), industrial forestry, and conversion of lands to other uses such as agriculture. Although direct habitat loss through development within boreal forests is comparatively low, habitat loss in deciduous forests is considerable due to greater human use.

Habitat loss results in forest fragmentation that influences the activities of individuals, species demographics, and interactions among species. For example, fragmentation has resulted in parasitism of forest bird species by the brown-headed cowbird (*Molothrus ater*). Habitat fragmentation also can affect the demography of invertebrates. For example, increased fragmentation was directly related to the duration of forest tent caterpillar outbreaks in southern Ontario (Roland 1993).

Fragmentation is caused by expanding human populations and is initiated typically by dissecting landscapes with roads (Hunter 2002). Fragmentation has resulted in altered biotic diversity and community structure in forests. Examples are range expansion for species including red maple (*Acer rubrum*), opossum (*Didelphis virginianus*), and coyote (*Canis latrans*), in addition to population increases of other species (e.g., trembling aspen (*Populus tremuloides*), white-tailed deer (*Odocoileus virginianus*)). Fragmentation has also been associated with population or range declines for species including many neotropical migrant birds. Invasion of forests by exotic species (e.g., garlic mustard, brown-headed cowbird) is facilitated by fragmentation.

Fire/Fire Suppression

Fire is an important component of many forest systems and is necessary for their maintenance. Fire is important for nutrient cycling, succession dynamics, and has been a factor in the evolution of plant and animal communities. In the Great Lakes region, fire is an integral component of the boreal and jack pine forests and also influences deciduous forests. Fire can be initiated naturally (e.g., lightning) or anthropogenically (e.g., prescribed burn, accidental). In fact, people have used fire since the mid-Pleistocene to manipulate ecosystems to achieve desired benefits (Pyne et al. 1996). These two means of ignition have the capacity for periodicity which can exert an evolutionary, consistent effect on biota. Fire plays a major role in maintenance of early successional forest stands and perpetuation of some forest types (e.g., oak savanna).

Large-scale fire suppression has been conducted for most of the 20th century. Suppression is conducted typically to protect human life and property. Fire suppression alters forest succession by favoring climax seral stages. Climax seral stages have lower biotic diversity and reduced nutrient cycling as a greater proportion of nutrients are tied up in mature trees. Fire suppression can also result in unnatural fuel loading. Human ignited fires in areas of fire suppression can have catastrophic consequences. For example, 5,000 ha of Point Reyes National Seashore burned in 1995, damaging or destroying 48 homes and costing $6.2 million to fight. This fire originated from an illegal campfire and burned in an area with high fuel loading due to decades of fire suppression (U.S. Department of the Interior 1995 in Barbour et al. 1999).

Harvest

Harvest can include extraction of timber, animal, plants and plant parts (e.g., berries). Although in part related to Habitat Loss/Fragmentation and Fire/Fire Suppression, harvest was separated to emphasize the importance of resource extraction on forests. Use of trees has increased with human population growth and is essential for construction, and paper products. Timber harvest results in forest fragmentation, causes a net loss in nutrient availability, and affects community and successional structure. Timber harvest is likely the dominant form of resource extraction in forests. During a 20-year period, 12.7 million ha of timber was harvested in the Great Lakes region alone (Barbour et al. 1999). An example of effects of timber harvest on forest fragmentation was demonstrated for Newfoundland. Due in large part to logging, forest stand size in this province decreased from 200 ha during the 1950s to 10 ha during the 1980s (Holling 1987). Although logging does not occur on lands managed by the National Park Service, the effects of logging may be observed from harvest that occurs adjacent to these lands. For example, intensive logging could result in fragmentation and isolation of National Park units from adjacent habitat.

Other forms of harvest include hunting and trapping of wildlife. Many species of wildlife including gray wolf (*Canis lupus*), fisher (*Martes pennanti*), and American marten (*Martes americana*) were numerically reduced or extirpated in portions of their range within the Great Lakes region (Johnson 1984, Theil 1994, Winebar 1995). Hunting is allowed on several park units within the Great Lakes Network. Harvest has contributed to altered trophic relations, biotic diversity, and genetic integrity of several species.

Insects/Disease

Insects and disease are critical factors in forest dynamics. Through defoliation or direct mortality, insects and disease can have major effects on forest succession, diversity, trophic relations and demography of species. The effects of insects and disease may not be expressed for years after initial infestation (Ricklefs 2001). In boreal forests, insects can affect areas as large as areas affected by fire. Hall and Moody (1994) estimated that forest losses (area in which overstory trees were killed) from insects in Canada were 1.5 times greater than losses due to forest fires. An example of the effects of insects and disease is the spruce budworm (*Choristoneura fumiferana*) outbreak which caused mortality of balsam fir and white spruce over 3.94 million ha in Ontario during 1992 (Howse and Applejohn 1993). Gypsy moths (*Lymantria dispar*) have defoliated large tracts of forest in eastern North America and are becoming more prevalent in the western Great Lakes area.

For this model, invasive exotic fungi, parasites, and their associated diseases are also included. An example is the introduction of an exotic fungal parasite transported to the New York area from Europe that virtually eliminated chestnut (*Castanea dentata*) in eastern North America. Another example is beech bark disease, which refers to a complex consisting of a scale insect and 2 fungi (McCullough et al. 2001). Beech scale was accidentally introduced to Nova Scotia in 1890 from Europe and has spread eastward to the eastern Upper Peninsula.

Climate/Weather

Climate is the major determinant of plant distribution (Barbour et al. 1999), with temperature and moisture the most important variables. Perturbations of climate, such as El Nino, have profound effects on forest communities. Human activities have caused an increase in concentrations of greenhouse gases, particularly carbon dioxide, which is increasing temperature globally (Clark 1986). An effect of global warming is increased stress on trees and other vegetation, particularly those in the boreal forest. This additional stress increases vulnerability of trees to insect and disease outbreaks (Holling 1987). Increased temperatures also reduce moisture content of soil and woody debris resulting in reduced productivity and increased prevalence of fire. Precipitation abundance and distribution also effects availability of some nutrients for plants and this influences primary production.

Wind (e.g., tornadoes, storm events), resulting in tree windthrow, can substantially influence forests by altering nutrient budgets, community structure, and aspects of landscape pattern. For example, high winds in the Boundary Waters Canoe Area Wilderness in 1999 resulted in 100s of hectares of windthrow. This event resulted in high fuel loading and altered fire management including consideration of mechanical removal of trees and prescribed fire.

Herbivory

Herbivory is the act of consuming portions of, or entire plants. Herbivory is subdivided into grazing, or consumption of herbaceous vegetation and browsing, or consumption of woody vegetation. The most common type of plant-herbivore relationship is termed the interactive herbivore system. In this system, herbivores influence growth rates and subsequent fate of vegetation (Ricklefs 2001).

Although herbivores rarely consume >10 percent of forest vegetation (Ricklefs 2001), herbivore population irruptions have had substantial effects on forest communities. Spruce budworm, gypsy moth, and tent caterpillar outbreaks have defoliated large forested areas. Increasing white-tailed deer populations have altered diversity and composition of forest plant communities throughout eastern North America, including the Great Lakes region (Stromayer and Warren 1997, Waller and Alverson 1997).

ECOSYSTEM ATTRIBUTES

Ecosystem attributes are a parsimonious subset of biological, physical, and chemical elements of the system and are representative of overall ecological conditions of the system. In this model, in addition to presenting characteristics of these ecosystem elements, we also address multiple levels of biological organization (e.g., biotic diversity, succession) and processes (e.g., trophic relations, primary production) either directly or indirectly.

Physiology/Organism Health

Some attributes of physiological processes and organism health are indicative of stress on ecosystems and therefore useful for long-term monitoring. Contaminant-induced biochemical processes provide evidence that organisms are being exposed to contaminants. For example, exposure to heavy metals stimulates cellular production of metallothionein, a protein used to regulate essential metals in many organisms. Cellular damage is minimized because the toxic metal is sequestered by metallothionein and effectively removed from circulation (Klaverkamp et al. 1991). Analyses for contaminants that accumulate in specific tissues of organisms provide information about exposure. In addition, altered rates of growth and reproduction, essential for population viability and species persistence, are indicative of anthropogenic stress (e.g., Beyers et al. 1999).

Soil Characteristics (chemical and physical)

We define soil to include both organic and inorganic components of the forest floor. Soils are integral to biogeochemical cycling of nutrients, affecting decomposition and primary productivity. Soil quality and chemistry is affected by climate (e.g., weathering), weather (e.g., windthrow), harvest (e.g., nutrient removal, erosion, compaction), and fire (nutrient enrichment or loss). Lowered soil nutrient levels can result in reduced primary productivity due to plants increasing root systems and active transport which decreases above ground plant growth.

Factors affecting physical soil characteristics include habitat loss and fragmentation, harvest, and climate. Habitat loss from development modifies soil structure through compaction which alters soil water-holding capacity. Erosion or soil compaction is typically increased during timber harvest or when forests are converted to agriculture. Loss of the nutrient-rich organic layer due to erosion affects primary productivity. Also, subsequent soil temperature changes affect other processes/attributes such as decomposition. Earthworms can also dramatically alter physical characteristics of soil (Hale 2004).

Landscape Pattern

We define landscape pattern as the juxtaposition of different vegetation types across a landscape. Quantifying landscape patterns temporally and spatially defines the degree of fragmentation that has occurred (Peterson and Parker 1998). Fragmentation can be characterized by patch size, shape, and juxtaposition on the landscape. Habitat patch size will influence which species can successfully colonize or maintain viable populations within patches. Patch shape will determine habitat edge which has been associated positively (e.g., increased species diversity) and negatively (e.g., brown-headed cowbird parasitism) with ecosystem attributes. How habitat patches are juxtaposed on a landscape affects dispersal and movements of organisms between patches. Fragmentation can also be characterized by landuse pattern (e.g., forest, agriculture, residential, roads). Fragmentation and landuse pattern in combination will have major effects on forest systems. The altered landscape pattern created by humans through development and harvest has frequently had adverse effects on distribution and abundance of numerous species (Robbins et al. 1989, Haila 1999).

Population Demographics

Demography includes the rate of growth of populations, both temporally and spatially. This attribute is essential for understanding viability of species. Population demography includes characteristics such as natality, mortality, density, and dispersal. Factors affecting demographics include pollutants and chemicals, invasive exotics, habitat loss, fragmentation, and harvest. Pollutants and chemicals can affect the physiology of individuals and subsequently, their survival or reproductive potential. Invasive species can compete with indigenous species by reducing habitat availability and suitability. Habitat loss reduces the total amount of area available to species to maintain populations. Fragmentation of habitat has been demonstrated to affect movements (including dispersal) and reduce habitat suitability for many species including black bear, fisher, and American marten. Direct harvest of a species can alter age structure, sex ratio, and population size.

Biotic Diversity

In addition to the inherent value of maintaining native diversity in ecological systems [it] is important for stabilizing ecosystem function. Diverse systems are better able to maintain productivity under stress or environmental perturbations (Tilman and Downing 1994, Tilman et al 1997). Human-induced causes for altering biodiversity include habitat reduction, fire/fire suppression, fragmentation, harvest, and introduction of exotic species. Habitat reduction can eliminate species directly, reduce population size, and affect dispersal which can adversely affect species viability. Similarly, fragmentation alters habitats which results in colonization of other species in addition to providing pathways for non-native invasive species. Harvest, particularly overharvest, can affect species viability and alter other demographic parameters (e.g., sex and age structure). Exotic species can initially increase biotic diversity (through addition of species) but frequently reduce diversity ultimately through competition with native species. For example, competition between spotted knapweed (*Centaurea maculosa*) and native vegetation on the Grand Sable Dunes in Pictured Rocks NL presently threatens native vegetation including populations of federal and state-listed Pitchers thistle (*Cirsium pitcheri*) and Lake Huron tansy (*Tanacetum huronense*), respectively.

Succession

Succession is a directional change in species composition or structure of a community or system over time. The word directional implies that species that once dominated the area will not return to dominance unless a disturbance occurs that reinitiates succession. Stage (or sere) of succession is defined by the biotic community present in time. Examples of anthropogenic factors that affect succession include habitat loss, fire, and harvest. Natural factors include insect or disease outbreaks, fire, and regional weather patterns (e.g., windthrow). Habitat loss alters succession and can prevent succession for extended periods (e.g., urban development, agricultural crops). Some types of timber harvest (e.g., clearcutting or shelterwood cuts) can prevent climax seral stages. Insects, disease, and windthrow can set back succession by defoliating or felling canopy trees. The effect of fire on succession depends in part on fire type (e.g., ground, canopy) and intensity.

Trophic Relations

Trophic level refers to groupings of organisms as determined by their primary feeding or energy assimilation relationships. Broad examples of trophic levels include plants (primary producers), herbivores, carnivores, and detritivores. Understanding trophic relations is critical to documenting energy flow and nutrient cycling through a system. Examples of trophic relations include competition, herbivory and predation. Anthropogenically-induced alterations of trophic relationships can have adverse effects on forest ecosystems. For example, conversion of forests to agriculture has resulted in burgeoning white-tailed deer populations throughout the eastern United States. Consequent herbivory of deer has altered the composition and structure of herbaceous and woody vegetation in remaining forests (Waller and Alverson 1997).

Primary Production/Decomposition

Ecosystem processes, and the biogeochemical cycles they control, are fundamental attributes of all ecosystems. Primary production is the assimilation of energy and production of organic matter by photosynthesis. Primary production of plants and other photosynthetic autotrophs form the base of all food chains. Primary production is critical because it determines the total energy available to the ecosystem. Natural (e.g., light, temperature, water) and anthropogenic (e.g., timber harvest, human development) factors can significantly influence primary production. All plant species have optimal ranges of natural conditions that allow maximum productivity. Deviations from these optimal ranges will reduce photosynthesis and subsequent primary production. Timber harvest affects primary production by removing trees which produce considerable organic matter. Timber harvest can also increase primary production by creating openings that enhance production of understory vegetation.

Decomposition is the rate at which carbon and some other elements/nutrients are metabolized and made available for primary production. Decomposition rates affect primary productivity through the amount of nutrients made available. Decomposition is affected by both natural (e.g., climate, fire) and anthropogenic (fire, timber harvest) factors. Temperature directly affects microbial activity which enhances decomposition. Fire can accelerate decomposition through burning organic material; however, extremely high-temperature fires can release nutrients into the atmosphere, making them unavailable to local forest systems.

Examples of Potential Monitoring Questions

Relationship of environmental contaminants to organism health. What are the primary sources of environmental contaminants and what are the primary means that allow their entrance to forests? What are the environmental contaminants most likely to affect forest ecosystems? What levels of these contaminants cause detectable changes in forest processes? Which species are best suited for monitoring contaminant levels? What is the extent of lateral transfer of contaminants from aquatic to forest ecosystems?

Relationship between human activities and landscape alteration. What are the dominant human activities in the western Great Lakes and within park units? How much area do they represent and how are they juxtaposed on the landscape? What is the current level and rate of change of fragmentation in the Great Lakes network? What is the relative degree of isolation of park units within the network and which human activities are major causes of isolation? What is the extent of connectivity between park units and what are current threats to these corridors?

Relationship between human activities and species and community diversity. What is the present level of biotic diversity within each park unit and how does this diversity compare to similar areas outside of parks? Does fragmentation appear related to source-sink populations for species or restricted species dispersal patterns? Are their apparent patterns of invasion of exotic species that could alter diversity or community structure? Are their relationships between anthropogenically-inflated populations of herbivores (e.g., deer) and plant community metrics? What are the relationships between wildlife harvest and population demographics? What is the estimated loss of habitat for select species in forest systems, i.e., what is realized versus potential habitat? What types of activities occur within parks and how do they vary spatially and temporally? What is the distribution and abundance of visitors in parks and how do they affect forest systems?

EXAMPLES OF BROAD METRICS OF STRESSORS

Pollutant/chemical loading
Sources of pollution,
Distribution pattern
Identification of pollutants
Trends in chemicals known to be highly toxic
Chemical use/unit area

Non-native invasive plants
Distribution
Abundance, Community diversity
Pathways of invasion

Habitat loss/fragmentation
Human population trends
Land use patterns, Recreation/visitation trends
Human development patterns (e.g., urban growth, road construction, agriculture)

Fire/Fire suppression
Historic, present, and future fire patterns
Causes of fire (i.e., natural, anthropogenic)

Harvest
Distribution and abundance of harvested resources
Harvest rates

Characteristics of harvested populations (e.g., age/size class, sex ratio)

Insects/Disease
Distribution and abundance of species
Outbreak frequency, timing, duration

Climate/weather
Evaporation
Transpiration
Wind patterns
Temperature
Precipitation

Herbivory
Herbivore composition, abundance, distribution
Prey species composition, abundance, distribution
Biological diversity indices

EXAMPLES OF BROAD METRICS OF ATTRIBUTES

Physiology and Organism Health
Histology
Bioaccumulation
Growth rates
Reproduction

Soil Characteristics (Chemical and Physical)
Nitrogen/phosphorus pools
Organic layer
Erosion
Temperature
Water storage
Soil structure

Landscape Pattern
Patch characteristics (e.g., size, shape, juxtaposition)
Connectivity
Edge
Population Demographics
Recruitment (natality)
Survival (or mortality)
Density
Dispersal

Biotic Diversity
Species composition
Relative abundance

Succession
Regeneration
Structure
Replacement rates
Community type

Trophic Relations
Competition
Herbivory
Predation

Primary Production and Decomposition
Process rates
Biomass

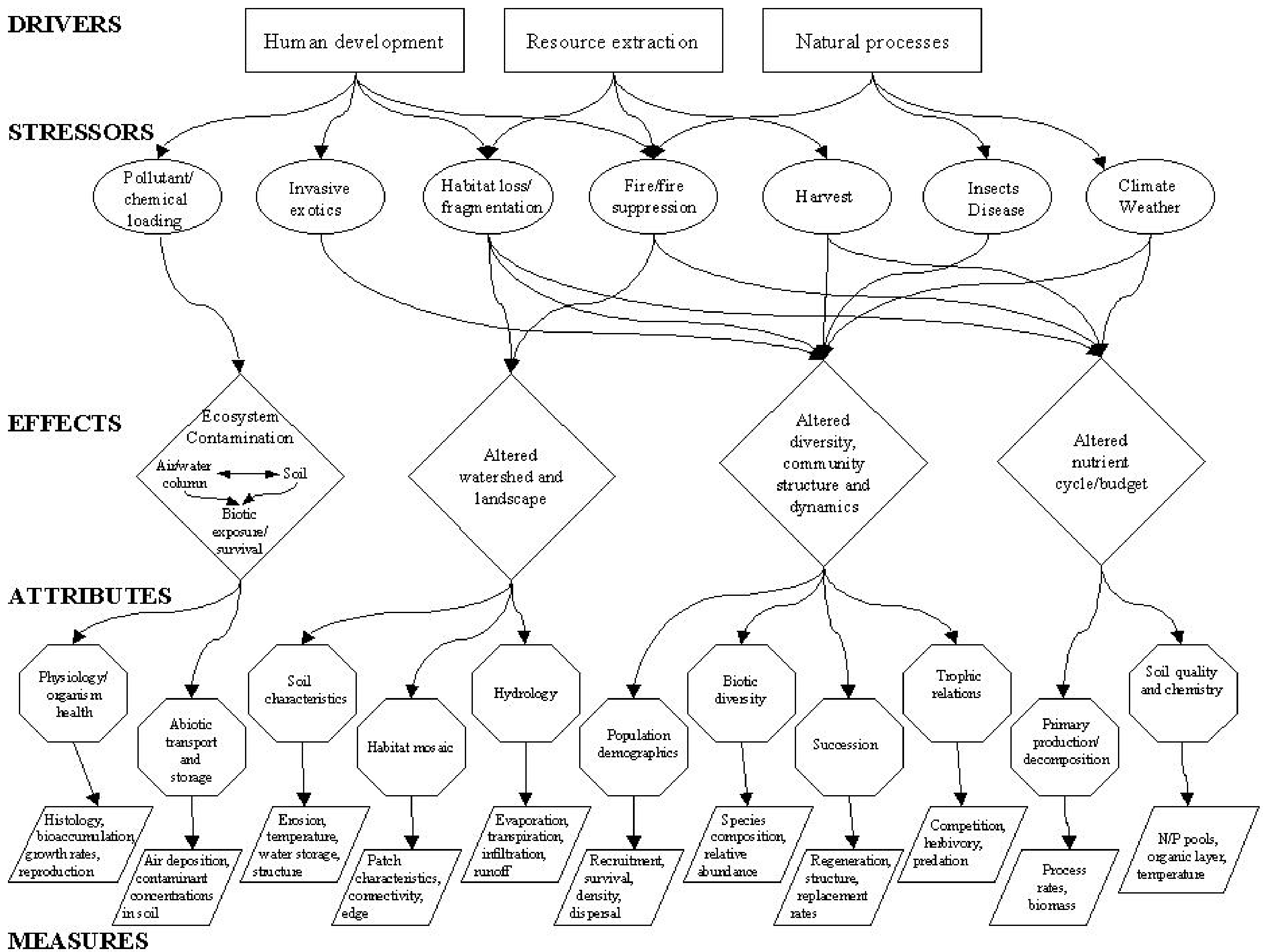

Figure 1. Great Lakes forest conceptual model. Model developed for the NPS Great Lakes Inventory and Monitoring Network of Parks to illustrate connections between selected attributes (Vital Signs) and system drivers.

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Great Lakes Network Wetlands Conceptual Model

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INTRODUCTION

The term wetland is a generic descriptor of a wide variety of places, including marsh, wet meadow, swamp, bog, fen, and muskeg. The commonality among these environments is the presence of standing water or saturated soils during at least a portion of the growing season. Many definitions exist for wetlands, both for regulatory purposes (e.g., the federal Clean Water Act, the Food Security Act, and state definitions) and for ecological purposes (e.g., Cowardin et al. 1979, Finlayson and Moser 1991, National Research Council 1995, Warner and Rubec 1997). Recent ecological definitions recognize the crucial elements of hydrology, soils or substrates, and vegetation. The following U.S. Fish and Wildlife Service definition by Cowardin et al. (1979) is currently widely accepted:

> *"Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water…wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes, (2) the substrate is predominantly undrained hydric soil, and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year."*

Wetlands exist in places where surface water periodically collects for some time or where a high water table is sufficient to saturate soils. Such places include depressions surrounded by upland, with or without a drainage system; relatively flat, low-lying areas along major water bodies; shallow portions of large water bodies; and sloped areas below sites of groundwater discharge.

Although wetlands cover a relatively small portion of the world's land surface (approximately 4-6 percent, Mitsch and Gosselink 2000), their ecological and societal values are disproportionately great. Some of these values are flood storage; sediment retention; improvement of water quality; shoreline stabilization; erosion control; habitat for plants, fish, and wildlife; biodiversity reservoir; groundwater recharge; and food web production and export (Maynard and Wilcox 1997, Tiner 1999). Wetland-dependent shellfish, fish, waterfowl, furbearers, and timber provide important and valuable harvests and recreational opportunities. On a global scale, wetlands contribute to stable levels of available nitrogen, atmospheric sulfur, carbon dioxide, and methane. Wetlands provide important habitat for a large percentage of the species on the U.S. threatened and endangered species list. For example, 28 percent of the plants, 68 percent of the birds, 75 percent of the amphibians, 66 percent of the mussels, and 38 percent of the insects on the threatened and endangered species list are associated with wetlands (Mitsch and Gosselink 2000).

Despite the obvious benefits of wetland environments, they have been extensively modified or destroyed by human activities. In the contiguous United States, approximately 53 percent of all wetlands have been lost in the last two centuries (Mitsch and Gosselink 2000). The states within the Great Lakes Network are no exception, with Minnesota losing 42 percent, Wisconsin losing 46 percent, Michigan losing 50 percent, and Indiana losing 87 percent of their wetlands (Mitsch and Gosselink 2000). This widespread destruction of wetlands was accomplished through draining, dredging, filling, diking, peat mining, mineral and water extraction, and water pollution. Until the 1970s, U.S. government policies encouraged wetland draining through legislation such as the Swamp Land Act and the Agriculture Conservation Program (Mitsch and Gosselink 2000). Currently, wetlands are the only ecosystem type that is comprehensively regulated across all public and private lands within the United States (National Research Council 1995). The federal Clean Water Act, Section 404, provides protection of wetlands across the nation, but each state has jurisdictional authority to add further requirements. Despite current legislation and policies, wetland losses have continued (Environment Canada 2002). Urban development, rural development, and agriculture accounted for 30 percent, 21 percent, and 23 percent, respectively, of these losses over the past two decades (Dahl 2000).

Wetland Classification

Numerous classification systems have been developed for wetlands, but the system adopted by the U.S. Fish and Wildlife Service (Cowardin et al. 1979) is the one most commonly used by scientists worldwide (Mitsch and Gosselink 2000). This classification system is hierarchical and all-encompassing, including both freshwater and marine systems. Riverine, lacustrine, and palustrine wetland systems exist within the Great Lakes Network parks. Definitions adapted from Cowardin et al. (1979) are as follows (specifics related to salinity are not included, as they are not relevant to wetlands in the Network):

> *Riverine system*s are linear features that include wetlands and deepwater habitats contained within a channel of (usually) flowing water. Riverine wetlands are not dominated by trees, shrubs, or other persistent vegetation, but may be dominated by non-persistent vegetation or be unvegetated.
>
> *Lacustrine systems* include wetlands and deepwater habitats > 8 ha that occur in topographic depressions. Persistent vegetation other than submerged aquatics covers < 30 percent of the total area (but non-persistent vegetation may cover >30 percent). Similar wetlands < 8 ha may be included in this system if the water depth is greater that 2 m during low water times or if at least portions of the boundary contain wave-formed or bedrock shorelines.
>
> *Palustrine systems* are wetlands dominated by persistent vegetation. Wetlands without persistent vegetation are also included in this system if they are < 8 ha, < 2 m deep during low water times, and no portion of the boundary contains wave-formed or bedrock shoreline.

These three large systems encompass several subsystems and numerous classes and subclasses of wetlands, described in greater detail below. Systems, subsystems, and classes of wetlands are defined largely by their geology, hydrology, and to a limited degree, vegetation (e.g., upper perennial, rocky shore; limnetic, unconsolidated bottom; littoral emergent wetland). Subclasses are further defined by generic vegetation types (e.g., persistent and nonpersistent emergent wetlands, broad-leaved deciduous, and needle-leaved evergreen forested wetlands).

Common terms for different wetland types, such as marsh or swamp, usually correspond to one or more types as defined by Cowardin et al. (1979) (Table 1). For example, a marsh would be a lacustrine or palustrine, persistent or nonpersistent, emergent wetland; an open canopy bog would be a palustrine moss-lichen wetland, or if it contained black spruce (*Picea mariana*) trees, it would be a forested, needle-leaved evergreen wetland; a black ash (*Fraxinus nigra*) swamp would be a forested, broad-leaved deciduous wetland.

Most wetland ecologists recognize three broad classes of Great Lakes coastal wetlands, based on hydrogeomorphology and shoreline processes: *lacustrine, riverine*, and *barrier-protected* (Environment Canada 2002). *Lacustrine* coastal wetlands are directly influenced by water level fluctuations, nearshore currents, and ice scour. They may be open to the lake, in broad bays or along the shoreline (*open lacustrine*), or somewhat protected in a bay or by a sand spit (*protected lacustrine*). Rivers and streams flowing into the Great Lakes may contain *riverine* coastal wetlands. They may be *drowned river mouth* wetlands, formed where river current velocity slows as the river enters the Great Lake, or they may be *delta* wetlands, with alluvial deposits extending out into the lake. *Barrier-protected* coastal wetlands develop behind a barrier beach (*barrier beach lagoon*) or behind a series of beach ridges (*swale complexes*). They may be connected to the lake through a channel, or they may be isolated from direct lake influences while maintaining subsurface connections (Keough et al. 1999).

Within each of these general coastal wetland classes, a complex mosaic of wetland types often exists consistent with the Cowardin et al. (1979) classification system. Brief descriptions of these wetland types occur below.

Common Wetland Types in the Great Lakes Network Parks

Emergent Wetland - Nonpersistent. Emergent wetlands with nonpersistent vegetation, i.e., plants that die back at the end of the growing season, occur in riverine, lacustrine, and palustrine systems. At certain times of year, this wetland type contains no obvious signs of emergent plant life. Examples of nonpersistent plant taxa include horsetail (*Equisetum fluviatile*), pickerelweed (*Pontederia cordata*), arrow arum (*Peltandra virginica*), and arrowheads (*Sagittaria* spp.).

Emergent Wetland - Persistent. Persistent emergent vegetation normally remains visible and standing throughout the year. Cattails (*Typha* spp.), sedges (*Carex* spp.), several bulrush species (*Schoenoplectus* spp.), and giant reed (*Phragmites australis*) are examples of persistent emergent plant taxa. Emergent wetlands with persistent vegetation occur only in palustrine systems.

Aquatic Bed. Aquatic beds consist of floating-leaved and submerged aquatic vegetation in wetlands and deepwater habitats. This wetland type occurs in riverine, lacustrine, and palustrine systems. Within the Aquatic Bed class, four subclasses (algal, aquatic moss, rooted vascular, and floating) commonly occur in Great Lakes network parks, described below.

Table 1. Comparison of general wetland types with the Cowardin et al. (1979) classification system.

General Wetland Type	Classification by Cowardin et al. (1979)
Marsh "An ecosystem of more or less continuously waterlogged soil dominated by emersed herbaceous plants, but without a surface accumulation of peat." (Lincoln et al. 1998).	• Riverine, Upper and Lower Perennial, Emergent Wetland, Nonpersistent • Lacustrine, Littoral, Emergent Wetland, Nonpersistent • Palustrine, Emergent Wetland, Nonpersistent
Bog "A peat-accumulating wetland that has no significant inflows or outflows and supports acidophilic mosses, particularly Sphagnum." (Mitsch and Gosselink 2000).	• Palustrine, Moss-Lichen Wetland, Moss • Palustrine, Moss-Lichen Wetland, Lichen
Fen "A peat-accumulating wetland that receives some drainage from surrounding mineral soil and usually supports marshlike vegetation." (Mitsch and Gosselink 2000).	• Palustrine, Moss-Lichen Wetland, Moss • Palustrine, Moss-Lichen Wetland, Lichen • Lacustrine, Littoral, Emergent Wetland, Nonpersistent • Palustrine, Emergent Wetland, Nonpersistent • Riverine, Upper and Lower Perennial, Emergent Wetland, Nonpersistent
Swamp "Wooded mineral wetland or peatland. Internal flow of water from margins or other mineral sources...Substrate often woody, well-decomposed peat, or a mixture of mineral and organic material..." (Harris et al. 1996).	• Palustrine, Scrub-Shrub Wetland, Broad-leaved Deciduous • Palustrine, Scrub-Shrub Wetland, Needle-leaved Deciduous • Palustrine, Scrub-Shrub Wetland, Broad-leaved Evergreen • Palustrine, Scrub-Shrub Wetland, Needle-leaved Evergreen • Palustrine, Scrub-Shrub Wetland, Dead • Palustrine, Forested, Broad-leaved Deciduous • Palustrine, Forested, Needle-leaved Deciduous • Palustrine, Forested, Needle-leaved Evergreen • Palustrine, Forested, Dead

Algal. The algal subclass of wetland may be dominated by mats of filamentous algae occurring on the bottom or floating to the surface, or by *Chara* or *Nitella*, two commonly occurring genera of algae that superficially resemble vascular plants.

Aquatic Moss. Aquatic mosses such as *Fissidens* and *Fontinalis*, and aquatic liverworts, also included in this subclass, grow most often on the substrate in riverine and lacustrine wetlands.

Rooted Vascular. Beds of rooted aquatic plants include floating-leaved species, such as water-lily (*Nymphaea odorata*), yellow water-lily (*Nuphar* spp.), and water-shield (*Brasenia schreberi*); and submerged taxa such as milfoil (*Myriophyllum* spp.), water-celery (*Vallisneria americana*), and pondweed (*Potamogeton* spp.).

Floating. Freely floating vascular plants that occur either on or beneath the surface are abundant in this subclass. Typical examples are duckweed (*Lemna minor, Spirodela polyrhiza*), bladderwort (*Utricularia* spp.), and coontail *(Ceratophyllum demersum*).

Moss-Lichen Wetland. Mosses or lichens dominate this class of wetland, with trees, shrubs, and forbs covering <30 percent of the total area. Moss-lichen wetlands occur only in palustrine systems. Moss wetlands, covered with species of peat mosses (*Sphagnum* spp.), occur in Network parks, while lichen wetlands do not.

Scrub-Shrub Wetland. This wetland type is dominated by woody species <6 m tall, including shrubs and young or stunted trees. Scrub-shrub wetlands occur in palustrine systems. Five subclasses of scrub-shrub wetlands, described below, exist in the Great Lakes Network parks.

Broad-leaved Deciduous. This subclass contains shrub species such as alder (*Alnus incana*), willows (*Salix* spp.), red osier dogwood (*Cornus sericea*), sweet gale (*Myrica gale*), winterberry (*Ilex verticillata*), buttonbush (*Cephalanthus occidentalis*), and bog birch (*Betula pumila*). Young trees such as red maple (*Acer rubrum*) and black ash are also typical.

Needle-leaved Deciduous. Tamarack (*Larix laricina*) is the only needle-leaved deciduous species to occur in the Network.

Broad-leaved Evergreen. Ericaceous species such as bog rosemary (*Andromeda glaucophylla*), Labrador tea (*Ledum groenlandicum*), bog laurel (*Kalmia polifolia*), and leatherleaf (*Chamaedaphne calyculata*) typically dominate broad-leaved evergreen wetlands.

Needle-leaved Evergreen. This subclass of wetland is dominated by young or stunted individuals of black spruce and/or white cedar (*Thuja occidentalis*) trees.

Dead. Dead woody species <6m tall dominate this subclass of wetland. Increased water levels that persist for prolonged periods, such as that produced by a beaver impoundment, may cause this type of wetland to form. Woody species may also die because of fire, herbicides, or a variety of other natural or anthropogenic causes.

Forested Wetland. Forested wetlands are dominated by tall shrubs and trees $\geq$6m tall. Typically they are structurally diverse, containing a tree canopy, a shrubby understory layer, and herbaceous ground flora. Often called bottomland hardwoods, cedar swamps, or black ash swamps, forested wetlands occur in palustrine systems. Four subclasses of forested wetlands exist in the Great Lakes Network (described below).

Broad-leaved Deciduous. Red maple, black ash, green ash (*Fraxinus pennsylvanica*), swamp white oak (*Quercus bicolor*), and American elm (*Ulmus americana*) are typical tree species characterizing broad-leaved deciduous wetlands.

Needle-leaved Deciduous. The only representatives of this subclass in the Great Lakes Network are wetlands dominated by tamarack.

Needle-leaved Evergreen. Black spruce and white cedar are the species that characterize this wetland subclass.

Dead. Dead woody species $\geq$6m tall dominate this wetland type. As with dead scrub-shrub wetlands, dead forested wetlands may result from prolonged increased water levels, disease, or other natural or anthropogenic causes.

In addition to the different vegetated wetland types described above, several classes and numerous subclasses of unvegetated wetlands occur in the Great Lakes Network. These wetlands are generally described by bottom or shoreline characteristics. For example, the *unconsolidated bottom* class includes the subclasses *cobble-gravel, sand, mud,* and *organic*. The reader may refer to Cowardin et al. (1979) for a description of all of the classes and subclasses of unvegetated wetlands.

Within the Great Lakes Network, the following parks have coastal wetlands: APIS, ISRO, SLBE, and INDU. All Network parks (those listed above, plus VOYA, GRPO, PIRO, SACN, and MISS) have a variety of inland riverine, lacustrine, and/or palustrine wetlands.

ECOSYSTEM DRIVERS

Natural and anthropogenic forces influence all ecosystems. Variation in climate and consequent hydrology, succession, herbivory, and fire are important natural processes controlling all wetlands. With the discovery of atmospheric contaminant deposition and global climate change, it appears likely that every ecosystem in the biosphere is or will be influenced by humans as well (Vitousek et al. 1997).

For the purposes of this model, 'Ecosystem Drivers' refers to the major natural and anthropogenic forces that influence wetland ecosystems. Anthropogenic drivers may disrupt natural processes (e.g., the presence of a harbor or breakwater interrupting the transport of sediments along the shoreline) or occur within the context of natural processes (e.g., the introduction of exotic species during periods of naturally low water levels).

Each ecosystem driver exerts ‘stressors’ on the ecosystem. The following definition of stress is used in this model: “…*a perturbation (stressor) applied to a system (a) which is foreign to that system or (b) which is natural to that system but applied at an excessive [or deficient] level.*” (Barrett et al. 1976). Agricultural pesticides are an example of a stressor foreign to wetlands. Nutrient enrichment and fire suppression are stressors applied at unnaturally high and low levels respectively. Wetland ecosystem drivers and stressors are shown graphically in Figure 1.

Natural Processes

Natural stressors to wetland ecosystems include changes in water levels, changes in sediment supply and transport, climate, weather, succession, and biological disturbances. Hydrology is the most important factor in wetland ecosystem maintenance and processes, affecting biogeochemical processes, nutrient cycling and availability, and biological communities (Environment Canada 2002). Addition of sediments to wetlands affects vegetation, water quality, and faunal communities. Transport of sediment along Great Lakes shorelines affects the connectivity of coastal wetlands to direct lake influences. Climate (which is also influenced by anthropogenic activities) affects the floral and faunal communities present in wetlands, as well as water levels. Weather introduces a number of possible disturbance events, such as ice scouring, wave action, and extreme storm events. Succession occurs in wetlands through the accumulation of organic matter, such as peat, and through directional changes in water levels. Several biological stressors may affect wetlands, such as the spread of invasive native plant species (e.g., reed canary grass (*Phalaris arundinacea*)), activities of beaver (*Castor canadensis)*, herbivory (e.g., insects, muskrat (*Ondatra zibethica*), moose (*Alces alces*), waterfowl), and disease.

Anthropogenic Influences

Anthropogenic stressors to wetland ecosystems include draining, filling, dredging, change in sedimentation, road crossings, shoreline modification, nutrient enrichment, toxic chemicals, water level stabilization, fire suppression, introduction of non-native species, and modification of climate. Many of these stressors are inter-related (e.g., a road crossing may restrict water flow from one part of a wetland to another, hence stabilizing water levels; road crossings increase the chance of introducing exotic plant species) and are due to agriculture and development or urbanization.

Each of the natural and anthropogenic stressors (above) and their ecological effects are discussed in the following section.

STRESSORS AND THEIR HYPOTHESIZED ECOLOGICAL EFFECTS

Change in Water Levels (Including Water Level Stabilization)

The magnitude, frequency, duration, timing, and rate of change of water levels are known as the hydrologic regime (Poff et al. 1997). Factors influencing the hydrologic regime include landscape position, soils, underlying geology, precipitation patterns, groundwater relations, and surface water runoff patterns (Tiner 1999). The hydrologic regime affects soil bio-geochemical processes, nutrient cycling, and nutrient availability. These processes, in turn, influence the biological communities that can be supported in a wetland. Hydroperiod - the duration, frequency, and timing of water level fluctuations - varies among wetland types and, in part, determines wetland type.

Flooding of wetlands and prolonged lowering of wetland water levels can both occur as part of water development and management programs. The degree and duration of flooding determines the kinds of vegetation that exist in a wetland. Flooding may cause a loss of emergent vegetation, which affects the benthic invertebrate community and allows increased resuspension of sediments through wind activity, which, in turn, leads to high turbidity (Chow-Fraser 1998). Prolonged draw-down of water levels reduces the areal extent of the wetland and promotes colonization of upland plant species. Water temperatures warm quickly in low-water conditions and may make the habitat unsuitable for some species of fish (Environment Canada 2002).

Coastal wetlands are known as pulse-stable, or stress-controlled ecosystems (Maynard and Wilcox 1997, Environment Canada 2002), as their continued existence depends largely on fluctuating water levels at multiple scales: daily (seiches), seasonal, annual, and long-term (decades or longer). Because many plants and animals are adapted to and depend upon fluctuating water levels, this positive stress maintains the long-term biodiversity of coastal wetlands (Environment Canada 2002). Stabilization of water levels reduces wetland extent and vegetation diversity (Wilcox and Meeker 1991, Wilcox et al. 1993).

Change in Sediment Supply and Transport

Sediment is comprised of mostly inorganic particles < 2mm in diameter, thus encompassing sand, silt, and clays (Wood and Armitage 1997). Although sediments are a natural part of most aquatic ecosystems, human activities have dramatically increased sediment inputs to lakes, streams, and wetlands. Most sediment enters wetlands through urban and agricultural runoff. Wetland sedimentation is a common result of highway construction (Mitsch and Gosselink 2000). When suspended in water, fine sediments increase turbidity, decrease light penetration, and decrease primary productivity. Low light penetration allows few (or no) aquatic macrophytes to grow, which, in turn, decreases the availability of substrate for invertebrates, reduces the quality of the habitat for fish nurseries, and ultimately leads to a depauperate assemblage of piscivorous fish species (Keough and Griffin 1994). Sediment particles < 63 µm in size are frequently adsorbed to by a variety of contaminants, especially nutrients and heavy metals (Wood and Armitage 1997). Consequently, sediments are an integral part of nutrient- and toxicant-related effects in wetlands. Excessive sediment accumulation can alter the hydrologic regime.

Some wetland types, particularly coastal wetland complexes, benefit from a moderate amount of sedimentation, *sensu* Connell's (1978) "intermediate disturbance hypothesis". Meeker (1993) showed that sediment loading at intermediate levels provided nutrients to vegetation communities without smothering them. Too much sediment, however, smothers young plants, or as described above, leads to low light conditions.

Transport of sediment along Great Lakes shorelines is necessary to maintain sand spits and barrier beaches that protect coastal wetlands from damaging wave action (Environment Canada 2002).

Climate and Weather

The climate within the Great Lakes Network varies considerably, from the temperate regions encompassing INDU, SACN, and MISS, to the boreal conditions existing at ISRO, VOYA, and GRPO. This variation in climate affects the length of the growing season, the amount of solar radiation, the number of degree days, and other factors that ultimately result in a gradient of vegetation communities from south to north.

As anthropogenic activities continue to alter global climate, the effects on wetlands are not entirely predictable but likely include altered hydrology and changes in vegetation communities.

A variety of weather-related disturbances affect wetlands, such as flattening of emergent vegetation during large wind events, uprooting of vegetation due to wave action, lowering of water levels during periods of prolonged drought, rising water levels during periods of extended rain, addition of sediment due to flood events, and the scouring of vegetation and sediments by ice. Storm events may breach the barrier of a barrier-protected coastal wetland, exposing the wetland to direct the effects of wind, waves, and water exchange with the Great Lake.

Succession

The dynamics of succession, or ecosystem development, have been documented in a variety of wetlands. Changes of the hydrologic regime, such as water level stabilization or sustained low water levels, promote the advance of upland vegetation into formerly wetland areas (Wilcox et al. 1993). The accumulation of organic matter, such as senesced plants and peat, alter wetland conditions such that formerly deep-water areas become shallower and may begin to host aquatic macrophytes or emergent vegetation. Moss wetlands may extend over open water areas, on the surface, creating quaking bogs (Mitsch and Gosselink 2000), which then allow the colonization of additional wetland plant species. Variation in climate, hydrology, and other factors maintain wetlands at intermediate states of succession.

Natural Biological Disturbances

Biological components of wetlands can exert strong stresses on the system. For example, accumulation of senesced plants can hinder water circulation. Beaver are considered “ecosystem engineers” (Power et al. 1996) because they directly alter water levels and circulation. Herbivory by muskrats, geese, and in ISRO and VOYA, moose can remove substantial amounts of plant biomass from wetlands, altering plant communities and hydrology (Mitsch and Gosselink 2000). Insects, can also affect plant communities, as is hoped with the introduction of the beetles (*Galerucella calmariensis* and *G. pusilla*) to control the exotic purple loosestrife (*Lythrum salicaria*).

Some native plant species, such as cattail (*Typha latifolia*), are known to be invasive and aggressive. These species may dominate a wetland to the exclusion of a diversity of other native species, reducing habitat complexity.

Draining, Filling, Dredging

Draining, filling, dredging, and ditching are human modifications specifically designed to dry out wetlands. By removing the source of water influx or hastening water outflow, wetlands are desiccated, and the land is used for urban development, highway construction, or agriculture. Levees are often constructed with the primary goal of preventing water from entering the former wetland area. This practice has led to farming and development in the floodplains of rivers, which has also caused widespread property damage and loss of life when rivers flood. Wetland obliteration and subsequent fragmentation of remaining habitats has disrupted metapopulation dynamics (Gibbs 1993) and is associated with declines in the diversity of wetland organisms (Lehtinen et al. 1999).

Road Crossings

Road crossings often isolate wetlands from their water source or bisect wetlands, greatly diminishing the exchange of water between the two portions of otherwise intact wetlands. The loss or alteration of water influx reduces inputs of sediments, nutrients, and plant propagules, and may hinder the movements of animals (including fish, amphibians, mammals, and waterfowl). Long-term changes in plant and animal community composition may result from road crossings.

Shoreline Modification

Breakwalls, riprap, dikes, revetments, and groins are examples of shoreline modifications. Such modifications can reduce the supply of sediments necessary for the maintenance of sand spits and barrier beaches that protect coastal wetlands and deflect wave energy farther downshore, causing erosion elsewhere (Maynard and Wilcox 1997). Shoreline modifications can also prevent the shifting of wetlands landward during high water periods, ultimately reducing the extent and diversity of wetlands and impairing their functioning (Maynard and Wilcox 1997). Movement of wildlife between uplands and wetlands is often hampered by shoreline modifications (Woodford and Meyer 2002).

Nutrient Enrichment

Eutrophication, caused by excessive inputs of nitrogen (N) and phosphorus (P) from nonpoint sources, is probably the most common reason for impairment of surface waters and wetlands. More than half of the rivers and lakes that currently fail to meet water quality standards are impaired by nutrients (U.S. Environmental Protection Agency 2000). The dominant source of nutrients in U.S. surface waters is nonpoint runoff from agricultural and urban areas (Carpenter et al. 1998). Excessive N and P can cause drastic changes in plant communities, such as enhancing growth of cattails and other clonal perennial plants, thereby reducing vegetation diversity. The most prominent effect of nutrient enrichment is a proliferation of algae, which can lead to a wide array of additional problems. Algal blooms can initiate a self-reinforcing feedback loop, described by Chow-Fraser (1998) as follows: high algal biomass leads to high turbidity, which reduces light penetration and hinders growth of submergent plants; lack of submerged vegetation represents a loss of fish habitat, especially that of piscivorous fish, resulting in a change in the fish community to favor more small fish that consume zooplankton; abundant small fish decimate the zooplankton community, which would otherwise graze on phytoplankton, allowing an abundance of algae. In addition to this positive feedback loop, high algal biomass causes fish kills as decomposition and respiration consume large amounts of oxygen. Aesthetic, recreational, and drinking water values are also reduced by eutrophication.

Toxic Chemicals

Toxicant, in this model, refers to any anthropogenic chemical that reaches wetlands and potentially elicits toxic effects on organisms, communities, or the ecosystem (Rand et al. 1995). Wetlands receive toxicant inputs from upstream water sources, direct releases from point sources, and aerial deposition. Polluted streams, runoff, and groundwater transport toxicants from adjacent or distant sources. Natural or artificial wetlands are often used specifically for filtering contaminants that are released directly into the system. Finally, wetlands receive toxicant inputs from aerial deposition, which has become recognized through widespread mercury contamination of water bodies (Wiener et al. 2002) and subsequent bioaccumulation through the food web.

The well-known ability of wetlands to assimilate contaminants and “purify” water (Mitsch and Gosselink 2000) is largely due to the perception that contaminants entering wetlands are eventually ‘locked-up’ in sediments and, therefore, benign to organisms. However, there is mounting evidence that contaminants buried in wetland soils and sediments are still available to biota and, therefore, threaten aquatic and terrestrial ecosystems (Landrum and Robbins 1990, McIntosh 1991). For example, up to 2 percent of the total amount of organochlorines present in a lake’s sediments was removed from the lake as sediment-dwelling insects emerged into the terrestrial environment. In turn, the contaminated insects became a source of contamination to aquatic and terrestrial food webs (Fairchild et al. 1992).

The impacts of toxicants are greatest on predatory species at the top of the food web, due to bioaccumulation and biomagnification. As toxicant exposure time or levels increase, organisms suffer malformations, tumors, stunted growth, lost reproduction, and eventually death. Faunal populations are therefore affected when sufficient individuals suffer toxic effects and alter population abundance, biomass, and productivity. Disproportionate losses of populations lead to changes in community composition and, conceivably, alterations in ecological processes. Additionally, the occurrence of toxicants in the food web affects human populations, and has resulted in fish advisories in many areas.

Fire Suppression

Fire is necessary for the maintenance of some types of wetlands (review by Kirby et al. 1988). Although humans suppressed fires through most of the 20th century, its importance in nutrient cycling and plant community dynamics is now recognized. Fire is still suppressed in wetlands near urban and many agricultural areas. As a consequence, many wetlands have become dominated by woody, often exotic, vegetation.

Exotic Species

The invasion of non-indigenous species seriously threatens wetland ecosystems nationwide (U.S. Congress 1993). Most invasive plant species in wetlands have escaped landscaping cultivation or were intentionally planted to stabilize sites already disturbed by human activities. Lacking natural enemies, many exotic species rapidly infest wetlands and displace native flora and fauna. Giant reed (*Phragmites australis*), Eurasian milfoil (*Myriophyllum spicatum*), narrow-leaved cattail (*Typha angustifolia),* and purple loosestrife are common examples of exotic wetland plant species. Purple loosestrife is probably the most well-known and widespread invasive plant that is degrading U.S. wetlands. Several parks (APIS, SACN, SLBE, and VOYA) in the Great Lakes Network are attempting to control the spread of purple loosestrife and eliminate current infestations. As with other invasive exotic plant species, purple loosestrife alters biogeochemical cycling and hydrologic regimes in wetlands, and it directly out-competes native plants.

Exotic fish, such as ruffe (*Gymnocephalus cernuus*) and carp (*Cyprinus carpio*) also affect wetlands. Ruffe were unintentionally introduced to the Great Lakes through release of ballast water and now inhabit coastal wetlands. Carp were introduced intentionally in the 1800s and have subsequently become widespread (Becker 1983). Ruffe out-compete yellow perch (*Perca flavescens*) and are less desirable as prey items to larger piscivorous species, causing a change in the fish community structure. The feeding habits and spawning activities of carp increase water turbidity, destroy submergent vegetation, and increase nutrient loading - all deleterious to wetland structure and function.

ECOSYSTEM ATTRIBUTES

Ecosystem attributes are biological elements or components of natural systems and are representative of the overall ecological conditions of the system. Wetland attributes are combined into four broad categories, with numerous examples listed within each category (Figures 1 and 2). A subset of these attributes can serve as indicators of ecosystem health.

Physical and Chemical Attributes

This category includes wetland functions, chemistry, and presence of toxicants. Examples include: hydrologic regime, and specifically, water level fluctuation; water chemistry; nutrient balance in water and sediments; primary productivity; decomposition; sediment supply, chemistry, and characteristics; turbidity; and the presence and concentration of toxins.

This set of ecosystem attributes is often interdependent and ultimately controls all other aspects of wetland ecosystems. Primary productivity depends on the nutrient balance and turbidity. Water level fluctuations, water quality, and turbidity will, in part, determine communities of macroinvertebrates. The health of predator species, such as piscivorous fish and bald eagles (*Haliaeetus leucocephalus*), is affected by the concentration of toxins. Habitat for wildlife (including amphibians, fish, mammals, and birds) is in large part vegetation, the composition of which depends on water level fluctuations and nutrient balance.

Attributes at the Individual and Population Levels

Examples of this attribute category include: organism physiology and health, the concentration of toxins in tissues, population dynamics of wetland-dependent animals, presence and abundance of species especially sensitive to contamination, and presence and abundance of exotic species.

Some animal species are known to develop abnormalities when exposed to toxicants (e.g., lesions or tumors on fish and beak deformities in colonial nesting waterbirds). Other species may experience declines in reproduction or recruitment (e.g., snapping turtle (*Chelydra serpentina serpentina*) and bald eagle (Environment Canada and U.S. EPA 2001)). Still other animals may bioaccumulate toxins without exhibiting any immediate direct effects (e.g., otter (*Lontra canadensis*), T. Doolittle, pers. comm.), but may affect human consumption advisories (e.g., fish with dangerous levels of PCBs and mercury) or affect growth rates (e.g., common loon (*Gavia immer*) Kenow et al. 2003). Wetland-dependent species, such as amphibians, exhibiting stable populations may be an indication of a healthy wetland ecosystem. The presence of exotic species such as sea lamprey (*Petromyzon marinus*), purple loosestrife, Eurasian milfoil, and common carp has deleterious effects on native species presence and abundance.

Community Attributes

This attribute category includes the area covered by different vegetation types (e.g., submergent, emergent), plant and animal community composition, native and total biodiversity, and biotic community indices.

Changes in the area of vegetation types and changes in the plant community composition may be due to changes in hydrology, nutrient enrichment, sediment supply, presence and abundance of exotic species, and other attributes. Emergent, submergent, and floating aquatic plants, as well as algae may change in response to these other attributes. Animal community composition may be affected indirectly by changes in plant communities (both areal and composition) or presence and abundance of exotic species, or more directly through other attributes such as concentration of toxins, water chemistry (e.g., anoxic conditions), turbidity, and hydrology. While the validity of wetland community biotic indices remains in question for coastal wetlands (Wilcox et al. 2002), doubtless such indices prove valuable for some inland wetlands (Simon et al. 2001).

Attributes at the Landscape Level

The size, position, and number of wetlands, as well as land use and land characteristics in the vicinity of wetlands are examples of this category. These attributes, often measurable through an analysis of a series of remote sensing or aerial images, can affect other attributes at the community, individual and population, and physical and chemical levels. Sediment supply (e.g., through erosion), concentration of nutrients and toxins (e.g., through nonpoint and point source pollution), changes in hydrology (e.g., through dams, shoreline stabilization, dredging, diking, and flooding), introduction of invasive species, and metapopulation dynamics (e.g., through vicinity of and corridors between wetlands) may all be affected by landscape level attributes.

Increasing the percent cover of impervious surfaces within a watershed will increase runoff and the sediments, nutrients, and toxins carried by runoff. Shoreline stabilization may decrease the areal extent of a wetland. Invasive species may be introduced to a wetland more readily if the wetland is surrounded by urban or agricultural land use. Fewer wetlands and loss of connective corridors between wetlands may contribute to population extinctions or genetic bottlenecks through restricted gene flow.

EXAMPLES OF POTENTIAL MONITORING QUESTIONS AND ASSOCIATED METRICS

Each example of a potential monitoring question is followed by one or more metrics that could answer the monitoring question(s).

Are water levels changing in a directional manner? Has the hydrologic regime been disrupted?
- Monitor water level fluctuations on a daily, seasonal, annual, and long-term (decades, or longer) basis
- Monitor duration and frequency of inundation
- Monitor mean water depth (monthly, seasonally, yearly)

Is the areal extent of wetland vegetation types changing?
- Compare aerial photos across time, delineating vegetation structural types (i.e., submergent, emergent, woody)
- Map (via GPS delineation) vegetation type boundaries, and compare coverage and boundaries (via GIS) over time

Is the vegetation community composition changing?
- Monitor plant species quantitatively (e.g., percent cover and frequency along permanent transects and/or quadrats)

Is water quality changing?
- Regular sampling of common water quality parameters, such as dissolved oxygen, pH, alkalinity, conductivity, temperature, turbidity, nutrients (e.g., C., N., P)
- Monitor biotic indices (e.g., diatom communities in surficial sediments, benthic invertebrates)

Are toxicant loads increasing, decreasing, or stable?
- Regular testing of water, sediments, fish tissue, snapping turtle eggs, otter tissue, loon blood
- Monitor frequency of external lesions and tumors on fish

Is the abundance of (a particular) exotic species increasing, decreasing, or remaining stable?
- Regular sampling to estimate or measure the relative biomass, percent cover, and/or frequency of occurrence of non-native to native species
- Are macroinvertebrate communities changing over time?
- Regular sampling of macroinvertebrate communities to compare community composition

Is species diversity changing within a wetland (alpha diversity)?
- Regular monitoring of bird, mammal, herptile, and plant species richness, diversity, abundance, and guild composition

Are there fewer wetlands as time passes?
- Compare aerial photos of land cover over time

Are nonpoint pollution loads increasing, decreasing, or stable over time?
- Regular monitoring of sediment inputs at key locations
- Use aerial photos to compare thermal differences over time (infrared may be especially useful), differences in percent of impermeable surfaces within a watershed over time, amount of construction (or other causes of bare ground and ground disturbances)

Is the amphibian community changing?
- Regular sampling of amphibian communities and concomitant measurement of required breeding habitat

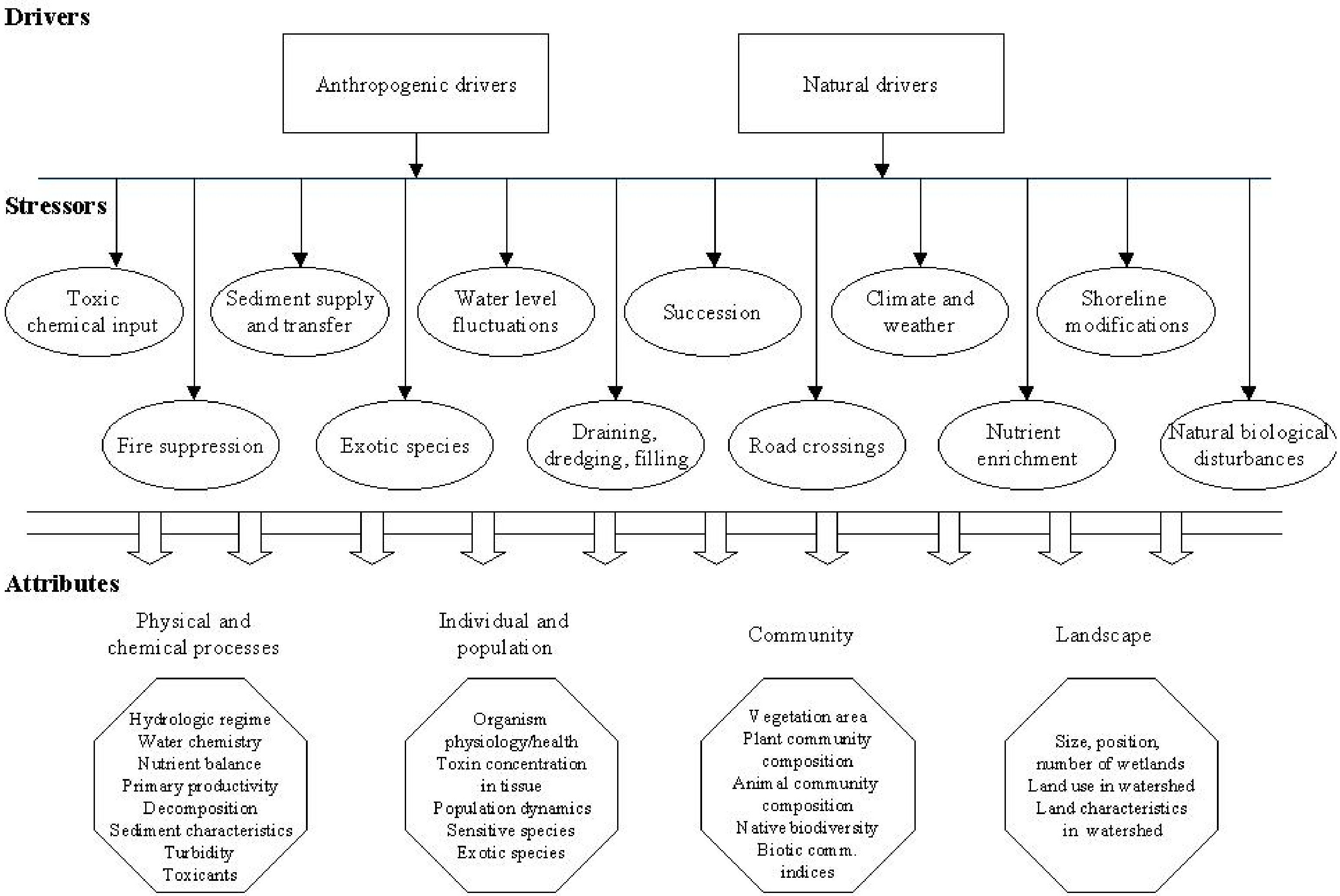

Figure 1. Great Lakes wetland conceptual model. Model developed for the NPS Great Lakes Inventory and Monitoring Network of Parks to illustrate connections between system drivers (rectangles) and attributes (octagons).

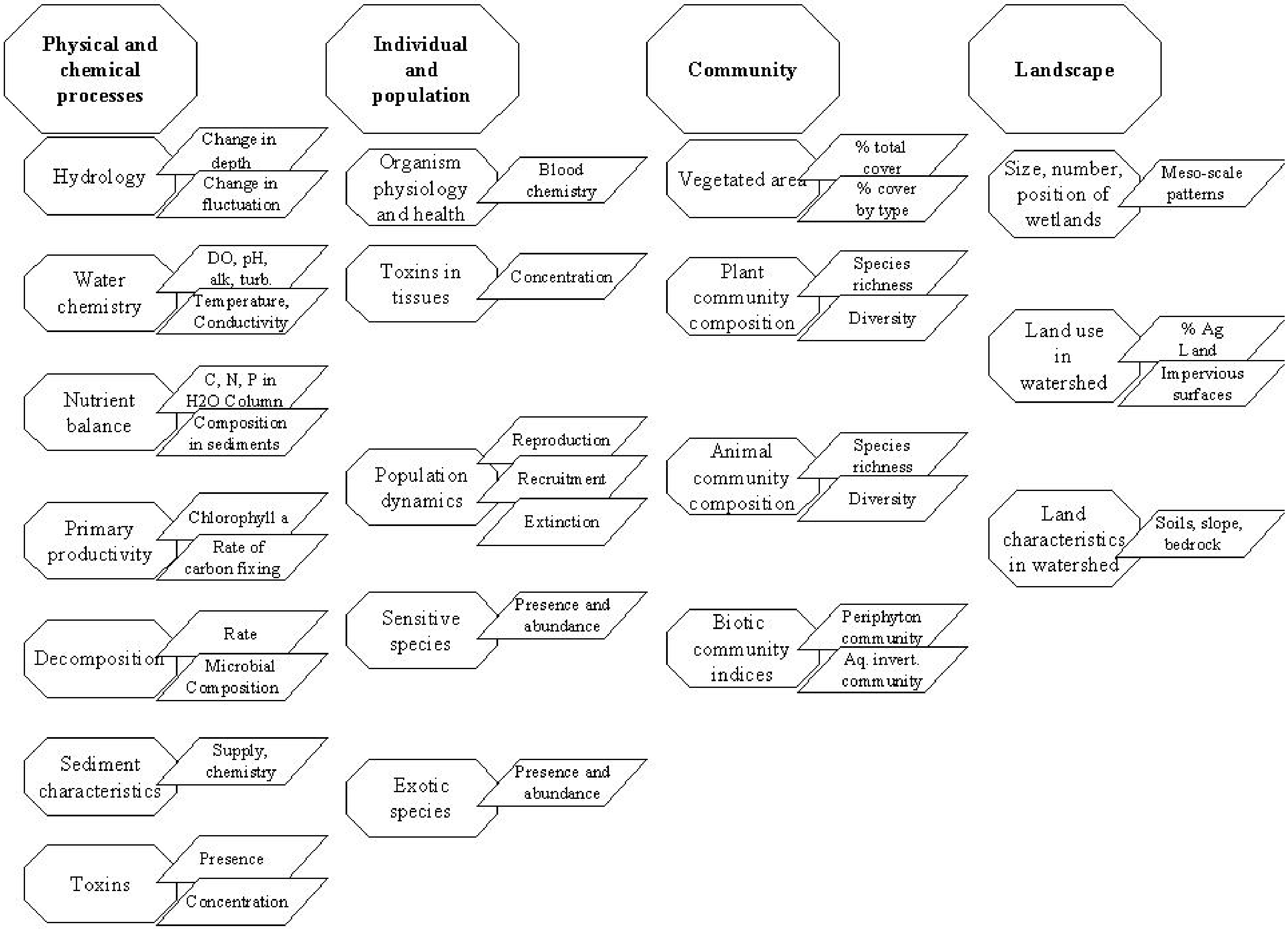

Figure 2. Great Lakes wetland conceptual model attributes and measures. Model developed for the NPS Great Lakes Inventory and Monitoring Network of Parks to illustrate subgroups within major attribute categories (octagons) and representative measures of attributes (parallelograms).

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Inland Lakes Ecosystem Conceptual Model

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INTRODUCTION

This narrative and accompanying conceptual model diagram are for the purpose of assisting the National Park Service (NPS) in the development of monitoring plans for inland lakes within the Great Lakes Network. The narrative and model follow the guidelines prepared by the NPS including terminology and symbols. The model and narrative are not intended to present detailed relationships of lake ecosystem components but rather a general presentation that highlights important influences and responses. The model will set the framework for more detailed discussion at focus workshops.

Inland lakes have for generations been highly valued for the recreational opportunities and esthetic experiences they provide. They have also attracted scientists for ecosystem studies because of their diversity, relative ease of isolating specific subunits, the ability to conduct ecosystem-level manipulations and more recently to use lakes for documenting changes in the global environment (Davis 1981). Because they are sensitive to inputs from watershed and air sheds, lake ecosystems in most or all areas of the world have likely experienced at least some level of human-induced, ecological change.

A conceptual model of a lake ecosystem to be useful must be general enough to address the diversity of lake types encountered at even a regional level. The diversity arises in the form of many features of lakes including:

Trophic status (oligotrophic, eutrophic, dystrophic…)
Annual mixing pattern (dimictic, polymictic, meromictic)
Morphometry (mean depth – volume/area, maximum depth, shoreline development, mean slope…)
Water Source (drainage lakes with inlet and outlet, seepage lakes with groundwater, no distinct inlet…)

Additionally, responses of lake ecosystems may vary considerably in duration depending on the sub system affected. Frost et al. (1988) emphasize the importance of recognizing the variations in scale in studying and understanding lake ecosystems. Hence lakes may show responses on evolutionary time scales (e.g. predator-prey associations) (DeAngelis et al. 1985) to time scales of seconds (phosphorus cycling) (Norman and Sager 1978). On intermediate scales, introduction of an exotic crayfish has been shown to alter the littoral community for several years (Lodge and Lorman 1987).

As certain lake types may respond more uniquely to given stressors, the narrative will identify and briefly discuss the basis for the expected response. Similarly when possible the narrative will identify times scales or expected duration of responses.

MAJOR HABITATS OF LAKE ECOSYSTEMS

The *pelagial zone* has long been the focus of lake ecology studies. This open water habitat supports the plankton community, the phytoplankton and zooplankton, as well as the ichthyoplankton. The phytoplankton are dependent on water motion for maintaining their position in the water column in addition to various adaptation in morphology of the cells to increase their surface area. Hence the phytoplankton will generally be distributed in the pelagial zone to the depth of mixing in the lake (in shallow lakes to the bottom, in stratified lakes to the thermocline) but functionally their effective distribution is a function of light, specifically the attenuation of light with depth. Phytoplankton photosynthesis is considered to prevail to that depth where about 1 percent of surface light remains, known as the compensation depth. Beyond this depth, respiration and decomposition processes exceed any contribution from photosynthesis.

In certain stratified lakes of sufficient clarity, the compensation depth may extend below the mixing depth into or below the thermocline. Photosynthetic production of oxygen can then help to create a habitat for cold water fishes in this layer, complementing the warm water habitat of the upper epilimnion. In other lakes, especially dark-stained, dystrophic lakes or hypertrophic lakes with high algal turbidity, the compensation depth can be shallower than the mixing depth producing a light limiting condition for production in the lake. The zooplankton, because of their mobility typically show variations in their vertical distribution from vertical migration in response to diurnal changes in light intensity in the water column. Factors influencing the underwater light regime are thus of considerable ecological importance in the ecosystem.

The *littoral zone* has been recognized as a major component of the ecosystem in recent decades. Wetzel (1979) showed the important role of detritus originating in submersed aquatic vegetation (SAV) of the littoral zone on the overall metabolism of the lake. Carpenter and Lodge (1986) stressed the important interactions of the littoral community; between sediment and water and between shoreline and open water. The major producers in this community, SAV, provide habitat and food for fishes, muskrats, waterfowl amphibians and invertebrates. Additionally, algal periphyton can be important contributors to to littoral production in certain lakes. The littoral zone includes a major nutrient pool that cycles slowly compared to the pelagial zone. It influences water temperature in shallow waters, reduces water movement and through self-shading increases light attenuation. Cole (1994) notes that the littoral community often has the highest biodiversity and biological production in the lake ecosystem. Schneider (1998), for example, collected a total of 95 invertebrate taxa in a study of the littoral zone of Green Bay.

The aerial extent of development of the littoral community is a function of the substrate, nutrient levels, and bottom slope of the nearshore environment. The depth distribution is a function of light attenuation and ultimately pressure, at least for angiosperm SAV. Hence factors decreasing light availability play a major role in the degradation of this community (Sager et al. 1996). Nutrients are also important for the growth of the SAV that seem to reach their maximum growth and biomass at roughly intermediate conditions between oligotrophic and eutrophic lake status (Wetzel 1979). Nutrient limitation in sediments and water seems to be in effect in oligotrophic lakes, while the light shading effect of increased phytoplankton biomass can limit depth distribution and growth in eutrophic lakes (Wetzel 1983).

The *profundal zone* includes the deep water, bottom sediment environment typically found in stratified lakes where it is a dark, cold habitat of low diversity. Processes of organic matter sedimentation and decomposition produce a physically uniform texture of the bottom sediments though the qualitative composition includes a range of inorganic and organic substances. In eutrophic lakes, the hypolimnetic water and sediments will have varying degrees of oxygen depletion while in oligotrophic lakes, oxygen depletion is minimal in the hypolimnion though oxygen depletion can occur in the pore water of the organically richer sediments.

In unstratified lakes of moderate depth, light may not reach the profundal sediments but with full mixing of the water column, bottom temperatures and oxygen levels will be comparable to the surface waters. Higher water temperatures consequently can have a positive effect on metabolism and growth on the benthos in these lakes. In shallow lakes, the littoral zone may prevail throughout the basin and a profundal zone is lacking. Maximum depth and trophic status thus are important influences on development of this sediment habitat among lakes.

In eutrophic lakes, the profundal benthos adapt in various ways to the oxygen stress and generally includes a few macroinvertebrates such as *Chironomous* (a dipteran larvae), some oligocheate worms, a small clam (*Pisidium*) and *Chaoborous* (another larval dipteran). In oligotrophic lakes the fauna associated with the profundal habitat is generally more diverse even though biomass and production may be lower than in eutrophic lakes. The profundal zone in oligotrophic lakes may include some of the same taxa found in eutrophic lakes but also the possum shrimp (*Mysis relicta*), a number of pontoporeiid amphipods and cold water fish such as lake trout and whitefish.

ECOSYSTEM DRIVERS

For this exercise, ecosystem drivers are considered to be major forces of change in ecosystems. For lake ecosystems, they typically, though not exclusively, operate from outside the lake basin and may be natural or anthropogenic and may have short-term effects of a day or have effects that last for years, decades or more. On paper it is easy to distinguish between natural and anthropogenic forces. In the real world, most lakes today are experiencing some level of anthropogenic influence while also responding to the ever-continuing variability of natural influences. The two are often difficult to distinguish.

Natural Processes

Hutchinson (1969) used the phrase “trophic equilibrium” to describe the close linkage between a lake and its watershed. The linkage is based on the geological character of the watershed, the fertility of the soil and bedrock, and the trophic status of the lake that through transport receives nutrients from the watershed. In the natural state and over the long term, this linkage would achieve an equilibrium condition. Major events such as extreme precipitation and runoff, fire and erosion would foster increases in nutrient loading or hydrological washout, leading to changes in the lake of varying duration. The point is that lakes are quite sensitive to events and process external to their basins. Features of the lake itself, such as basin morphometry, water clarity, and food chain structure, interact with the external influences to produce the lake ecosystem features as we see them.

Anthropogenic Influences

Watershed disturbances such as agriculture, urban development, logging and fire are major influences on lake ecosystems (Scrimgeour et al. 2001, Garrison and Wakeman 2000). Loss of protective vegetative cover on soil leads to increased loading of nutrients and sediments over the natural loads which stimulates increased growth of phytoplankton and submersed aquatic vegetation (SAV). These eutrophication processes can lead to excessive growth of nuisance algae, loss of SAV in the littoral community due to increased light attenuation and altered food chain processes and efficiencies owing to less palatable phytoplankton species (Richman and Dodson 1983, Sager and Richman 1991, Kemp et al. 2001)

Shoreline disturbances such as clearing emergent and submersed vegetation and removing woody debris to create swimming areas can lead to loss of aquatic habitat, decreased amphibian populations (Woodford and Meyer 2003) reduction in fish growth rates (Schindler et al. 2000) and decreased water quality (Garrison and Wakeman 2000).

Atmospheric deposition of contaminants illustrates the broad extent to which lakes are affected by factors external to the basin. The watershed area for a given lake in most cases is small in comparison to the air shed with the great distances substances may be transported before falling on the lake. Mercury is a problem in water bodies throughout the states and provinces of the Great Lakes area. Following deposition in the lake, inorganic mercury undergoes a transformation to methyl mercury, the form in which it bioaccumulates via the food chain. Animals, including humans and wildlife such as loons and eagles, that eat contaminated fish are susceptible to damage to the central nervous system. A primary concern is for human fetuses and newborn infants (ATSDR 1999). In the 1990s certain regions experienced a decline in mercury deposition rates that was followed by gradual declines in lake water and fish (Watras et al. 2000).

Deposition of oxides of sulfur and nitrogen produced from combustion of fossil fuels in coal-fired power plants, in automobiles and in other fuel burning processes causes acidification of lakes. Atmospheric transport of the sulfur and nitrogen oxides may be over great distances or from nearby sources. Not all lakes respond equally. The buffering capacity of lakes is set by the geological setting of the lake that determines the extent to which the lake ecosystem may be impacted by acid deposition. Other factors such as watershed gradient, vegetative cover, food web structure etc play a role in the lake's response.

Acidification of lakes is important for its broad ranging ecological affects as well as its influence on the methylization of mercury. The Clean Air Act Amendment of 1990 called for a decrease in sulfur dioxide emissions. Some acidified lakes are now showing recovery, others are not.

Recreation activities are increasingly regarded as a major influence on lake ecosystems. Considerable pressure from fishing and boating can lead to impacts on the age and size structure of fish populations and the food web (Reed-Andersen et al. 2000a; Landres et al. 2001, Harig and Bain 1998). Invasive and exotic species introductions can result from transporting boats from lake to lake inadvertently carrying entangled plant material and associated biota (Johnson 2001), for example, zebra mussels (Kraft et al. 2002, Reed-Andersen et al. 2000b) and Eurasion milfoil (Engel 1990). Similarly, organisms can be carried as bait for fishing and subsequently released, such as, rusty crayfish (Lodge and Lorman 1987, WASAL 2003). In most cases, successful invasive species have similar impacts, elimination of native species through predation and/or competition, alteration of habitats and modification of food webs.

Climate Change could become one of the most serious anthropogenic influences on ecosystems of all types. In the increasing number of scenarios and predictions being reported on the effects of climate change on lakes, just about all communities and processes show some response via effects of altered temperature regimes, hydrologic patterns and interactions with numerous other stressors. For inland lakes, geographic location may be important for temperature responses. Davis et al. (2000), based on interpretations of historical climate changes, suggest that inland lakes located near the Great Lakes may experience less extreme temperature effects because of the moderating effect of the large water bodies.

STRESSORS

Nutrient Loading

Inputs to lakes of the key nutrients nitrogen and especially phosphorus are generally considered to be one of the major influences on lake ecosystems. The lake response to changes in inputs is often fast consisting of a pulse in growth of the primary producers, especially the phytoplankton. Biomass turnover rates of the algae are typically high, on the order of 1 to 2 d^{-1} and the uptake and turnover rate of phosphorus by algae is even faster (Norman and Sager 1978). Movement of this growth pulse through the food chain is much slower of course as life cycles of organisms higher in the food chain are much longer. A sustained increase in nutrient loading will ultimately have some effect in the higher trophic levels. Anthropogenic disturbances in the watershed do increase nutrient loading, most of which is usually attributed to non point sources (Bennett et al. 1999, Klump et al. 1996, Carpenter et al. 1998). Cultural eutrophication leads to changes in phytoplankton species composition, size structure and growth rates all of which have relevance to the pelagial food web. The increase in algal biomass affects water clarity and the depth distribution of photosynthesis. The depth distribution and subsequently the aerial extent of the littoral community are generally reduced as well. Other effects of cultural eutrophication include impairment of esthetics and recreational values, loss of deep-water habitats and hypolimnetic oxygen depletion.

Sediment Loading

The loading of suspended sediments and detritus from the watershed is a function of soil temperature, moisture, hydrology and watershed morphology (Dillon and Molot 1997). In the absence of anthropogenic influences sediment loading may vary considerably, increasing as a function of natural catastrophe such as fire, floods, herbivory, etc which enhance soil erosion. With urban development, agriculture, logging, fire and other anthropogenic activities the watershed generally discharges an increased load of sediment and detritus to the lake. The impacts of increased levels of suspended solids include increased light extinction, thus exacerbating the nutrient loading effect on the underwater light climate from increased algal populations (Millard and Sager 1994).

Dystrophic lakes are a special case of allochthonous substance loading in which the lake accumulates dissolved and colloidal humic substances from a boggy wetland drainage basin. The water is brown stained with greatly reduced transparency, low fertility and generally low biotic diversity and production. The pelagic food web is characterized as based on bacterioplankton and the mobilization of energy from dissolved organic carbon compounds (Jansson et al. 2000).

Habitat Loss

Modification of the near shore environment is commonly seen in lakes where development of the surrounding area with cottages and homes has occurred. Removal of woody debris and emergent and submersed vegetation and installation of artificial structures drastically alter the environment. Habitat for amphibians, waterfowl, mammals such as beaver and muskrat and fish is often severely degraded or lost.

Metals/Toxic Loading

Mercury contamination in lake ecosystems experiencing aerial deposition of mercury can be found in most organisms and habitats of the lake (Boening 2000, Mackay and Toose 2003). In fish, mercury concentrations vary directly with size and age, indicating bioaccumulation through the food web (Glass 2001). As a result, fish of standard size at the top of the food chain (apex predators) are consequently used for comparison purposes in assessing mercury contamination in lakes (Kallemeyn et al. 2003). Effects of mercury contamination may be extended from the lake ecosystem through fish eating birds such as eagles, osprey and common loon and mammals such as river otters and humans (Mackay and Toose 2003).

Physiological effects of mercury relate to the fact that it accumulated in nervous system tissue. In humans, mercury exposure in pregnant women can lead to neurodevelopment effects in the fetus and child (Vahter et al. 2002). Consumption of contaminated game fish must therefore be closely controlled. In birds and other wildlife, physiological effects are difficult to ascertain in the field because of interacting effects of food, predation and presence of other types of contaminants (Karasov and Meyer 2000). In a general review, Boening (2000) notes that fish exposed to sublethal concentrations show a variety of physiological and reproductive abnormalities and that birds fed inorganic mercury showed a reduction in food intake and consequent poor growth. Boening also states that the form of retained mercury in birds is variable depending on species, location and target organ. Kallemeyn et al. (2003) reported elevated mercury levels in birds of Voyageurs National Park but that is was not known if their populations are being adversely affected. In a controlled study of great egrets, Spalding et al. (2000) reported that methyl mercury preferably accumulates in feathers, especially during fledging which may protect nestlings from adverse effects on growth until feathers cease growing.

Indicators of critical mercury concentrations have been recommended. Scheuhammer and Bond (1991) suggested feather concentrations of 20ug/g as a toxic effect threshold. Barr (1986) reported impaired loon reproduction when mercury residues in forage fish exceeded 0.3ug/g.

Atmospheric sources of other contaminants such as PCBs, PBDEs and other organochlorine compounds can be significant for inland lakes. Recent studies on Lake Siskiwit (ISRO) note the importance of long range transport and deposition. Green et al. (2000) noted highest PCB concentrations over Lake Michigan when winds are from the southwest (Chicago-Gary area) and when land surface temperatures are elevated. Kidd et al. (1995) observed high concentrations of toxaphene and other organochlorines in fishes from subarctic Lake Laberge, Yukon Territory. The authors determined the high concentrations resulted from biomagnification of atmospheric inputs. Bowerman (1993) found that productivity and reproductive success of bald eagles of the Great lakes and Voyageur National Park were significantly lower than in eagles of inland lakes.

Acid Deposition

Oxides of sulfur and nitrogen discharged to the atmosphere react with water vapor to form sulfuric and nitric acids that are deposited on the earth in acid rain or snow and fog. Effects on lake ecosystems depend on the buffering or acid neutralizing capacity (ANC) of the lake. Soft water lakes of low ANC (< 100 mueq/L) (Stoddard et al. 1998) have experienced declines in diversity of flora and fauna through reproductive failure or direct mortality. The Clean Air Act of 1970 and Amendment of 1990 were followed by emission reductions in North America and Europe that resulted in decreased sulfur depositions of up to 50 percent (Skjelkvale et al. 2001). On a broad scale of regions, Skjelkvale and colleagues found downward trends from 1989-1998 in sulfate concentrations in lakes of all regions with the low ANC sites showing the highest rates of recovery.

Certain lakes in northeastern US however have exhibited either no trend or further acidification in spite of strong decreases in sulfate levels due to decreases in soil base saturation in the watershed from earlier acid deposition (Stoddard et al. 1998, Lawrence et al. 1999). Similarly, certain lakes in Wisconsin are recovering while others remain acidic. The interaction of lake acidification processes and mercury appears to have a bearing on the uncertainty of recovery from mercury contamination (Watras et al. in press).

Exotic Species

Exotic, invasive species may be characterized by elevated fecundity, rapid growth and early maturity, typical traits of r-selected species where physiological tolerance is not a requirement for success (McMahon 2000). Their impact on lake ecosystems is one of a trend towards homogenization of the flora and fauna through direct processes of competition for food and space, predation and grazing and through alterations of the structure of food webs (Rahel 2002). Because of their still increasing numbers - the Great Lakes now have 161 exotic species according to Martin and Horns (2001) - they are regarded as one of the primary threats to biodiversity of the Great Lakes and inland lakes of the surrounding area. Prevention seems to be the only effective solution. Once established most are generally impossible to remove.

Fishing and Boating

Aquatic resources of national parks generally receive considerable recreation pressure from park visitors. Lakes and streams are prized for their remoteness and esthetics but subjected to various stresses, largely from fishing and boating. Pressure for providing adequate facilities and fishing opportunities has existed for many years. Fish stocking of native and non-native species to meet public demand may compromise some of the ecological values of lakes within national park boundaries (Landres et al. 2001). Harrig and Bain (1998) for example identified certain indicators of biological integrity that were sensitive to disturbance in Adirondack wilderness lakes including dominance of native fish species, relative abundance of *Daphnia*, size structure of the zooplankton and dominant taxa of the phytoplankton.

In Voyageurs National Park the maintenance of native, self-sustaining fish populations is made difficult by unauthorized fish introductions and release of non-native bait fish by fisherman (Kallemeyn et al. 2003). The authors noted in particular, the rainbow smelt, an exotic species, which because of its planktivorous feeding strategy has the potential to create a variety of ecological impacts. In Banff National Park, problems of non-native fish species stocking, loading of nutrients and road salts to certain surface waters and extirpation of key invertebrates from previously fishless lakes by stocked fish were reported by Schindler (2000).

Temperature and Precipitation Changes

It is probably beyond the scope of this report to review the many scenarios and predictions offered in relation to lake ecosystem responses to climate change. Some may wonder how lake managers can deal with this global phenomenon. Control of the stresses associated with it is out of our hands in many ways. Yet awareness of expected effects of climate change may be important when interpreting observations of changes in various lake ecosystem features. General scenarios indicate change towards warmer and drier climates in the century ahead (Davis et al. 2000). Translating the general into specific effects that can be attributed to climate change is not easy especially given the complex interactions of acidification, climate warming and increased UV exposure as a result of stratospheric ozone depletion (e.g., Schindler 1999).

One well documented trend is offered by Magnuson et al. (2000) with empirical evidence of historical change to a shorter duration of ice cover in lakes and rivers around the northern hemisphere. The change means higher surface water temperatures earlier in spring and later in fall. The potential effects are many, including the timing of important events such as fish spawning and hatching in relation to availability of plankton food sources, extent of oxygen depletion in an extended period of summer stratification, effects on habitats of cold-water fish species and on warm water species with limited ability to acclimate to higher temperatures.

Planning for ecosystem change may be the best strategy. Identification of reasonable scenarios for lake ecosystems and for expected changes in biotic and abiotic features will be important for lake managers (e.g., WASAL 2003, Magnuson et al. in press).

ECOSYSTEM ATTRIBUTES AND MEASURES

Attributes are any biotic or abiotic feature or process of the ecosystem that can be measured or estimated and that provide insights into the state of the ecosystem. These “emergent properties” may vary considerably in temporal scale, e.g., algal population growth versus fish species growth. Consequently interpretation of ecosystem response to stressors for example must be considered in the context of a suite of attributes that we assume will adequately represent the ecosystem. It is sometimes considered to be a reductionist approach hopefully based on firm knowledge. It is an approach that is open to the potential controversy of the scales of interest of observers that lead to distinct perceptions of the ecosystem depending, for example, on whether the interest is at a molecular level or ecological or evolutionary level (Schindler 1988).

Phytoplankton Community

Because of their fast growth rate, the phytoplankton response to stressors is on a short time scale. They are typically used as an indicator of trophic status in conjunction with others. Typical measures of the phytoplankton include chlorophyll *a* and taxonomic composition of at least the dominant species.

Zooplankton Community

The composition of this community reflects both the condition of the phytoplankton as its food source and the level of predation by planktivorous fish. Measures of the zooplankton include abundance, size distribution and taxonomic composition as an indication of top-down effects of the food chain.

Water Clarity

Water clarity is an indicator of trophic status, largely through effects of algae on light penetration. It may also be used to indicate the role of other particulates and dissolved substances (DOC) in light extinction. Measures of water clarity include Secchi disc transparency and determination of the light extinction coefficient.

Littoral Community

The aerial extent of this community and its diversity is an indication of the nutrient status and water clarity of the lake in addition to the slope and sediment composition of the bottom material. Measures include the taxonomic composition of the SAV and periphyton as well as the macro-invertebrate taxonomic composition and abundance.

Hypolimnetic Oxygen Deficit

The depletion of oxygen in the hypolimnion during summer stratification is an indication of trophic status. It is operative on a long time scale, representing one of the stable components of lake metabolism. The measure involves determination of the depth profile of dissolved oxygen at intervals through the stratification period.

Fish Community

The composition of the fish community in terms of age classes or size and trophic level can be useful for indicating fishing pressure, presence of exotic species, and food chain effects on zooplankton and algal abundance. Typical measures include taxonomic composition and functional feeding groups or trophic levels (e.g., piscivores, planktivores, etc).

Shoreline Habitat

This is an important habitat for juvenile fishes, amphibians, waterfowl, etc. Measures include assessment of woody debris, emergent and submersed vegetation, and amphibian and waterfowl/shoreline bird diversity.

Organism Health

Measures include growth and reproductive success and body burdens of contaminants (mercury, PCBs, etc)

Sediment/Water Quality

Routine monitoring typically includes samples of sediment and water for analyses of nutrients (total P, nitrogen species), a suite of metals, pH, acid neutralizing capacity, and contaminants including Hg, PCBs, and other organochlorine compounds.

Annual Temperature Regime

Determination of annual heat budget, summer temperature profile and duration of ice cover are useful measures for long term monitoring of climate change effects.

Lake Levels

Nearshore habitats which house a significant diversity of plants and animals may be severely impacted by unnatural water level fluctuations (Wilcox and Meeker 1991, Kallemeyn 1987). Regular monitoring of water levels can provide information on hydrological events, severe water level fluctuations, beaver dam activity and climate change.

The above list of measures is not ranked in importance. Monitoring strategies for different lakes will not necessarily include the same measures. Depending on the circumstances and conditions of the lakes, certain measures will be more appropriate than others. It is unlikely that all measures would be incorporated in a given plan. It remains for discussions in future workshops to decide on the best array of measures for monitoring the health of the lake ecosystem under consideration.

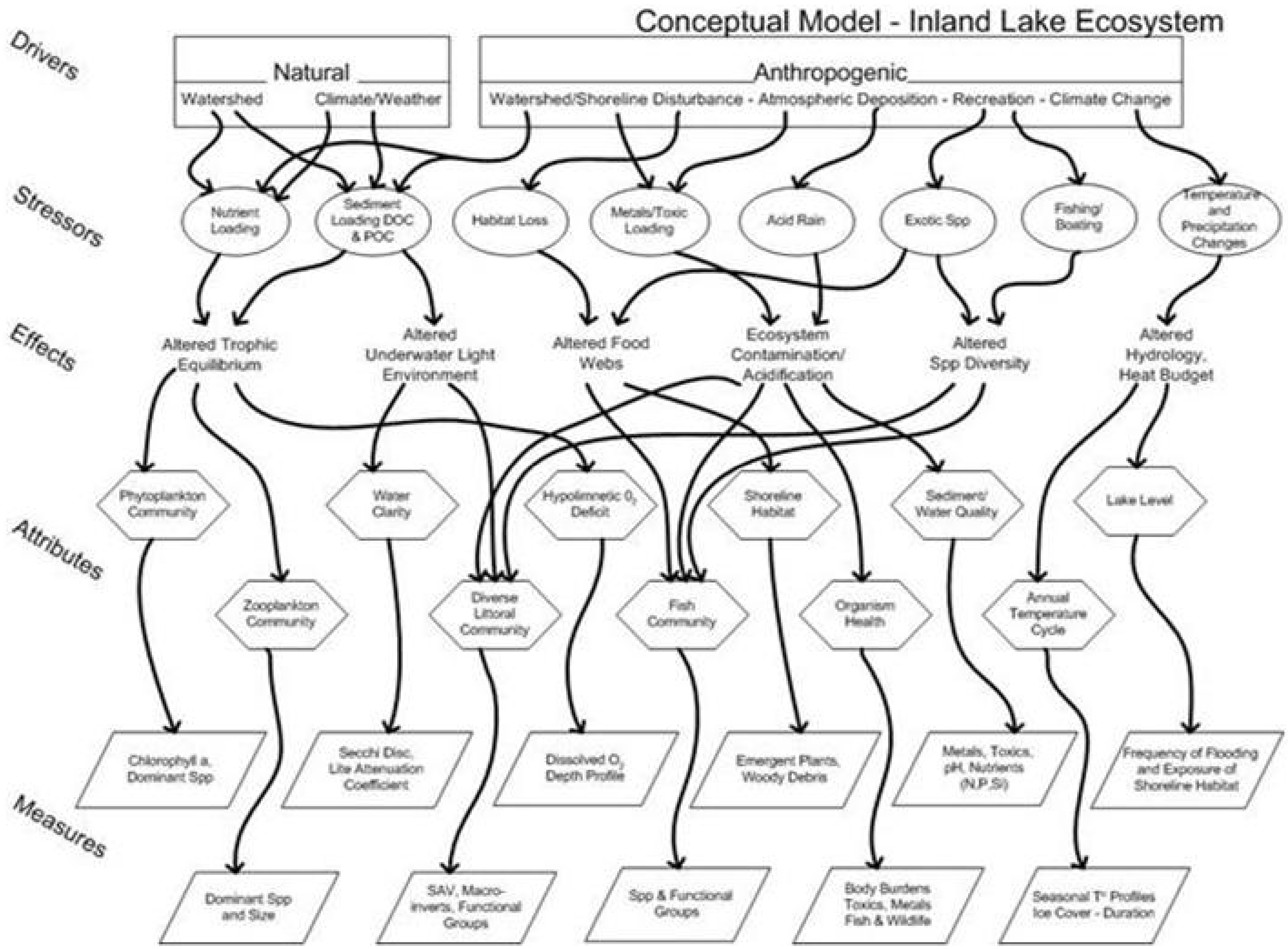

Figure 1. Great Lakes region inland lake conceptual model. Model developed for the NPS Great Lakes Inventory and Monitoring Network of Parks to illustrate connections from ecosystem drivers through stressors to attributes, as exhibited in specific measures.

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Large River Conceptual Model

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INTRODUCTION

The purpose of this report is to present a brief scientific description about large Midwestern river ecosystems, including:

their essential ecosystem characteristics and attributes (i.e., communities, habitats, species, and processes),
how characteristics and attributes interact with each other,
ecological services provided by large rivers,
connections between all of these and the natural and anthropogenic drivers that affect them at different spatial scales.

The description is accomplished by using a diagrammatic conceptual modeling approach that focuses on stressors (i.e., mechanisms of change caused by either natural or anthropogenic drivers) that are either foreign to the system or that occur outside of what we interpret as their natural range of variation. The model is intended to be a synthesis of current scientific understanding, field observations, and professional judgments regarding large river ecosystems.

The report is intended to assist the National Park Service (NPS) in developing monitoring plans for two riverine park units in the Great Lakes Network:

The St. Croix National Scenic Riverway (SACN), which protects 403.2 km (252 mi) of the St. Croix and Namekagon Rivers in northwest Wisconsin and eastern Minnesota.
The Mississippi National River and Recreation Area (MISS), which is a 115.2 km (72 mi) long corridor that follows the Mississippi River from the confluence of the Crow River, through Minneapolis/St. Paul, to the Goodhue County Line.

In addition, the report includes suggestions about vital signs of large river ecosystem health (Karr and Chu 1999) that can be considered as potential focal points of future monitoring programs at the riverine park units.

This report is not, however, intended to present regional details about the riverine park units or to rank the drivers and stressors by their level of importance. The river fundamentals presented here will be considered and merged with local information at a future workshop that focuses on the needs for and implementation constraints to monitoring in the Great Lakes Network.

SOME KEY ECOLOGICAL CONCEPTS ABOUT LARGE MIDWESTERN RIVERS

Most of the large rivers of the Midwest, like their counterparts worldwide, have been altered by a variety of human activities (Welcomme 1985, Dynesius and Nilsson 1994, Galat and Frazier1996). Humans have altered the physical templates of rivers, the hydraulic dynamics of their channels and tributary networks, and the land use characteristics of their basins. On such disturbed systems, management requires the restoration of altered system features to desired levels of quality (National Research Council 1992) and the conservation of river features that still exhibit desirable conditions.

Our scientific knowledge of large river ecosystems has expanded greatly over the last three decades. However, there is a great need to confirm many of our beliefs with data from rivers of the Midwest. The following concepts about river ecosystem structures, functions, and controlling factors are generally well accepted today by many river ecologists. Future monitoring within the riverine park units will probably support many of these beliefs, but we should expect to find that some of them will be incomplete. Future revisits to this conceptual model will thus provide an opportunity for work on the riverine park units to contribute to a better understanding of the class of ecosystem called large rivers.

The ecological condition of a large river depends on drivers and stressors that exist at multiple spatial scales (Frissell et al. 1986, Lubinski 1993, Naiman 1998). Drivers that operate at larger spatial scales tend to exert control over longer temporal scales and cycles (Poff and Ward 1990, Naiman 1998). Within a basin, as rivers increase in size in the downstream direction, predictable gradients occur in the forces that shape the stream, control the substrate, and provide organic material (Vannote et al. 1980).

Large rivers tend to be located at lower elevations than smaller streams within the same basin. They also often have shallower elevation gradients than their tributaries and therefore trap more sediment and have longer water retention times. These conditions, with the exception of local areas where the channel is constricted, generally result in lower water velocities and substrates dominated by finer particles. Under natural conditions, the discharge of a river increases with distance downstream. The predictability of the flow regime of a large river is typically greater than the predictability of its smaller, flashier tributaries (Johnson et al. 1995).

Under natural conditions, the primary sources of energy in a large river, detritus, fine particulate organic material, and attached bacteria, are usually allochthanous, that is carried downstream by tributaries. The River Continuum Concept (Vannote et al. 1980) holds that local photosynthesis in large rivers is limited by turbid water. However, the presence of dams, floodplains with large backwaters, or large amounts of woody debris in a given large river reach can reset energy processes to conditions more like those that occur in moderate size streams (Ward and Stanford 1983, Junk et al. 1989, Thorp and DeLong 1994, Bayley 1995). Under these conditions, in-stream (autochthanous) energy production through photosynthesis and increased invertebrate production increases.

In large rivers with substantial floodplains, annual flood pulses have been identified as perhaps the most important hydrologic feature that governs year-to-year changes in ecosystem productivity and possibly diversity (Junk et al 1989, Ward 1989).

Large rivers frequently exhibit distinctive reach or microhabitat characteristics that are attractive to individual or groups of species (Stalnaker et al. 1989, Montgomery and Buffington 1998). Reach distinctions frequently are reflected in different vegetation patterns, community types, and habitat assemblages (Lubinski 1993). Microhabitat attractions are often most clearly observed during specific life history stages, seasons, or discharge ranges. An especially important characteristic of large rivers is that conditions in their microhabitats change widely with river discharge (Reash 1999). Population changes in response to year-to-year variations in discharge are considered to be an important contributor to riverine biodiversity (Knutson and Klass 1997, Galat et al. 1998).

The flora and fauna of large rivers are adapted to and controlled in large part by the conditions discussed above. It is also important to keep in mind however, that large-scale distribution patterns of many species, terrestrial and aquatic, in the Midwest still reflect zoo-geographic patterns established by glacial land forming processes that existed thousands of years ago.

Large rivers, within the context of either their tributary networks or even broader spatial scales, function as landscape corridors (Lubinski and Theiling 1999). In this role, they provide ecological services such as removing wastes, and transporting nutrients, sediments and water itself, to systems downstream. The landscape corridor function of large rivers is of special value to migratory birds and fishes. This function may even extend beyond a river's basin, as in the case of the Mississippi River, which provides a migration corridor between continents for many waterfowl and neo-tropical bird species (Knutson and Klass 1997).

LARGE RIVER CONCEPTUAL MODELING

A variety of large river models have been developed that can be considered conceptual in nature (Amoros et al. 1987, Karr 1991, Lubinski 1993, Bayley 1995, Ward 1989). Although these models share many similarities, each contains unique elements, a result, in part, of the need to use the models for different purposes. The context and desired application of a conceptual model likewise determines its size, scope, and level of complexity. Guidance regarding the scope, elements, and detail of the conceptual model presented here was included in the project Scope of Work.

Modeling Natural Conditions

The purpose of conceptual models in development by the Great Lakes Network, is to "promote communication and integration among scientists and managers from different disciplines during the vital signs selection process." Consequently, we started constructing the conceptual model by considering natural large river attributes and their drivers. Karr's (1991) view of primary steam ecosystem elements (Figure 1) served as the basis for the six attributes (native species, biological interactions, channel/floodplain physiography, water flow, water quality, and energy flow) presented in the basic, undisturbed large river model (Figure 2). Geology, climate, and basin land cover have often been considered as primary drivers of streams and river ecosystems (Bhowmik et al. 1984, Resh et al. 1988). Under undisturbed conditions, each of the six attributes varies over time, responding to seasonal, annual and long-term changes in the three drivers. Water and sediment discharge regimes within the basin stream network provide the major mechanisms for the drivers to affect changes in the river attributes.

Natural disturbances, such as earthquakes, droughts or infrequent, channel-forming (i.e., one in five-hundred-year) floods, caused the attributes to depart from their 50-100 year range of variation (Sparks et al. 1990, Sparks et al. 1998). Native species however, being adapted to such disturbances, tended to return to pre-disturbance, system-wide population levels rapidly, even if their distribution shifted across fine spatial scales.

Definitions in use by the NPS distinguish between attributes and vital signs. Not all attributes are considered to be vital signs. Vital signs are defined as a subset of system attributes that is particularly information-rich and indicative of the quality, health, or integrity of the ecosystem. In the National Park Service's proposed monitoring operation, vital signs are intended to track changes in a subset of park resources and processes. Cairns et al. (1993) recognized that indicators could, in addition to functioning in trend detection, also serve in early warning and diagnostic roles. The NPS emphasis on the trend detection functional role of attributes was critical to developing the decision process for their selection.

Given the emphasis on trend detection, and the need to narrow the number of large river attributes to a set that could function in an operational monitoring program, we dropped two attributes, biological interactions and energy flow, from further consideration. These attributes have not been quantified extensively in large rivers, and the lack of strong data sets or routine methods for these attributes makes it difficult to consider them as viable trend detectors. However, should the NPS consider including diagnostic and early warning functions in a comprehensive adaptive assessment and management program (Harwell et al. 1999, Walters et al. 2000, Bisbal 2001), strong arguments can be cited (Bunn et al. 1999) for finding the extra resources required to treat these attributes as vital signs.

We should also note that when resource management is the responsibility of many organizations, selection of ecosystem attributes to direct a monitoring program also requires the support of partners. Harwell et al. (1999) referred to ecosystem features that are jointly regarded as important by the scientific community and the public as “essential ecosystem characteristics.” If the NPS develops its monitoring programs for SACN and MISS to include the information needs of outside partners, more attention will need to be directed at active public participation in identifying ecosystem values, services and conceptual model elements.

ATTRIBUTES FOR CONSIDERATION AS VITAL SIGNS

Native Species

In large rivers, native species include resident species that remain in place throughout the year and migratory species. The management of migratory species requires special attention to spatial scale, as the migration corridor function provided by the river can be vulnerable at any point along the corridor, not just at monitoring locations.

The pulsing nature of a large Midwestern river, which typically floods from April through June, results in complex patterns of species habitat use patterns. One researcher has dubbed the floodplain, not inaccurately, as a natural time-share condominium. Large river biodiversity, though difficult to quantify because of the sampling scales involved, is frequently considered high relative to smaller streams. A few selected studies have begun to provide the data to support that perception (Knutson and Klass 1998, Shiel et al. 1998, Schiemer 1999). The tendency for larger rivers to support more fish species than smaller rivers within a stream network is well known (Welcomme 1985).

Floodplain/Channel Physiography

This attribute refers to the physical template, aquatic and terrestrial, over which river water flows. Under natural conditions, the physical structure of any given river reach is determined by its gradient and water and sediment regimes (Montgomery and Buffington 1998). Floodplain/channel physiography contributes to what we generally think of as habitat, but it is a system attribute, whereas habitat is defined by the species or guild of interest. Not all large rivers have floodplains, but when floodplains are present they play an important role in sediment transport and deposition, carbon and nutrient recycling, the distribution of species, and the availability of food (Ward 1989).

Water Flow

Because of its ecological importance, water flow in large rivers has sometimes been referred to as a “master” variable (Richter et al. 1997, Poff et al. 1997, Galat and Lipkin 2000). Together with floodplain/channel physiography, it is a major determinant of where species can be found in the large river system. Water flow includes multiple variables, including discharge, velocity, and water level elevation.

Water Quality

By water quality, we include temperature and the natural compounds, gases and other constituents that would naturally be present in the water column of a large river. Key water quality variables that control ecological processes or species behavior in large rivers include temperature, dissolved oxygen, suspended and bed sediment loads, dissolved and suspended carbon, and nutrients. Water temperatures play a great role in controlling the reproductive timing and success of river fishes. Low dissolved oxygen concentrations can make certain areas of the river unsuitable for use by fish and may occasionally cause fish kills. Sediment not only plays a role in fluvial dynamics and the succession of riverine plant communities, but also controls (with plankton) the turbidity of river water, which can limit the amount of photosynthetically active radiation available to submersed plants. For this model, we considered any foreign material in river water as a stressor (contaminant), rather than as an element of water quality.

Adding Anthropogenic Model Elements

After identifying natural large river attributes and drivers, we identified the anthropogenic drivers and stressors that frequently control attributes and the overall condition of large river ecosystems. Figure 3 displays the drivers and stressors discussed most often in the literature, as well as their perceived connections to attributes.

Most large rivers, including those of the Midwest, have been altered by a relatively large number of anthropogenic drivers. Thus, it should not be surprising that Figure 3 contains 10 anthropogenic drivers operating though nine stressors. Table 1 provides additional details regarding the types of processes and human activities included in driver categories.

The connections shown between the drivers, stressors, and attributes in Figure 3 are intended to convey a high probability of effect in any large Midwestern River. However, the relative importance of the connections may differ substantially from one reach to the next, or from one time or flow period to another. Valuable discussions of such changes in connection strength are only possible when extensive local information about the river reach of interest is available. Such discussions for the SACN and MISS are anticipated at a future National Park Service workshop.

Table 1. Examples of drivers for large Midwestern river ecosystems.

Driver type	Driver–Coarse Level	Driver–Fine Level
Natural	Geology	Sub-basin geology Sub-basin soils
	Climate	Precipitation episode shift Annual/seasonal precipitation Annual/seasonal solar radiation
	Basin land cover	Sub-basin vegetation
Anthropogenic	Agriculture Barge traffic Barrier removal	Purposeful introductions Unintended introductions Inter-basin water transfers
	Global warming	Increased temperature More variable weather extremes Greater floods
	Point source pollution	Industrial wastes Municipal wastes
	Structural changes–main stream	Training structures Hydropower dams Navigation dams Floodplain development Dredging and filling
	Structural changes–tributaries	Channelization Hydropower dams
	Resource exploitation	Fish, mussel, timber harvests Mining quarrying
	Recreation	Boating Hunting, fishing
	Urbanization	

It is also beyond the scope of this conceptual modeling exercise to present a detailed discussion of each anthropogenic driver and stressor that affects large rivers. However, the comments below regarding selected driver and stressors are worth noting because of their potential relevance to the proposed monitoring programs.

Notes Regarding Selected Anthropogenic Stressors

Substantial reaches of SACN and MISS are already in areas of intensive urban development. The general movement of people from rural to urban communities is expected to continue into the foreseeable future, and urban sprawl can be expected to continue as well. This will place not only additional stress on NPS riverine units, but greater demand from the public to protect these resources.

No general discussion about the large river ecosystems of the Midwest can be complete without mentioning the increasing incidence of great floods over the last 60 years (Wlosinski 1999). The location of the SACN and the MISS in the more northern end of the Upper Mississippi River Basin, above the basin areas that have undergone the greatest agriculture conversions, may reduce (relative to southern rivers) their risk to flood damages, but that risk is still noteworthy. Future management of large Midwestern rivers to promote their ecological values cannot be accomplished in isolation from the issue of flood risk.

Increasingly, programs of the U. S. Army Corps of Engineers, the National Resources Conservation Service, and the U. S. Environmental Protection agency are considering major investments throughout the Mississippi River basin to reduce nutrient enrichment into large rivers and the Gulf of Mexico. In a program being developed for the Upper Mississippi River, The Nature Conservancy focuses on abating threats from “stressor” tributaries, and conserving the contributions of “reliever” streams that remain relatively undisturbed from agricultural stressors. Monitoring within SACN and MISS could provide considerable insight regarding the relative effectiveness of efforts to control nutrient runoff from stressor tributaries, and to sustain desirable land use conditions existing in basins that retain more of their natural land cover.

VITAL SIGN AND STRESSOR MEASURES

Figures 4 and 5, respectively, illustrate measures of fine-level attributes and stressors that are applicable to large Midwestern rivers generally, and to SACN and MISS specifically. These measures are proposed to begin evaluating the costs of monitoring within the park units,

As with the earlier discussion of the relative importance of different drivers and stressors, continued dialog about vital sign and stressor measures requires more detailed knowledge of spatial heterogeneity within the park units. That knowledge is necessary to begin developing an efficient and effective monitoring design that would yield scientifically valid data, and information that is relevant to management decisions.

Notes Regarding Measures

Large river ecosystems include terrestrial, aquatic and transitional communities (Junk et al. 1989). The selection process of native species groups for monitoring should include consideration of how these communities respond to drivers and stressors that operate at local, as well as systemic scales.

Measurement frequency should be based not only on the natural temporal variability of the vital signs, but also on the frequency of the anticipated stressor activity. As a result, while we might anticipate that many large river assessments will be required at annual intervals, others may be more appropriate at 5-10 year intervals. Still others may be event triggered, for example, during and closely following a major flood.

Point measurements in a large river are difficult to interpret and may have little value in describing overall system condition. Some repetition and randomness in the monitoring design is necessary to allow statistical inferences to larger (meso-scale) defined areas. However, the defined areas must also be relevant to potential management actions.

During the anticipated future dialog on monitoring, attention should be given not only to the value of each individual measure, but to the comprehensiveness of the information that is likely to be generated by the suite of selected measures. The suite of measures should reflect system condition equally as well as each measure reflects the condition of an attribute.

Effective design of an ecosystem monitoring program should at a minimum allow for the detection of trends. Documenting causality is a much more difficult task. The conceptual model presented here suggests that many anthropogenic drivers and stressors are probably affecting the health of the riverine park units concurrently. Complex ecosystem responses, uncontrollable circumstances, and uncertainties can therefore be expected to prevent any future ecosystem monitoring program from providing clear cut answers to questions about causation. However, coupling a well designed monitoring program to a complimentary set of controlled studies, may permit the teasing apart of some of the most important causal relationships that operate within a specific large river reach. An approach that incorporates monitoring and research to generate answers to different kinds of questions will enable managers to explain as well as describe the major changes affecting park unit resources.

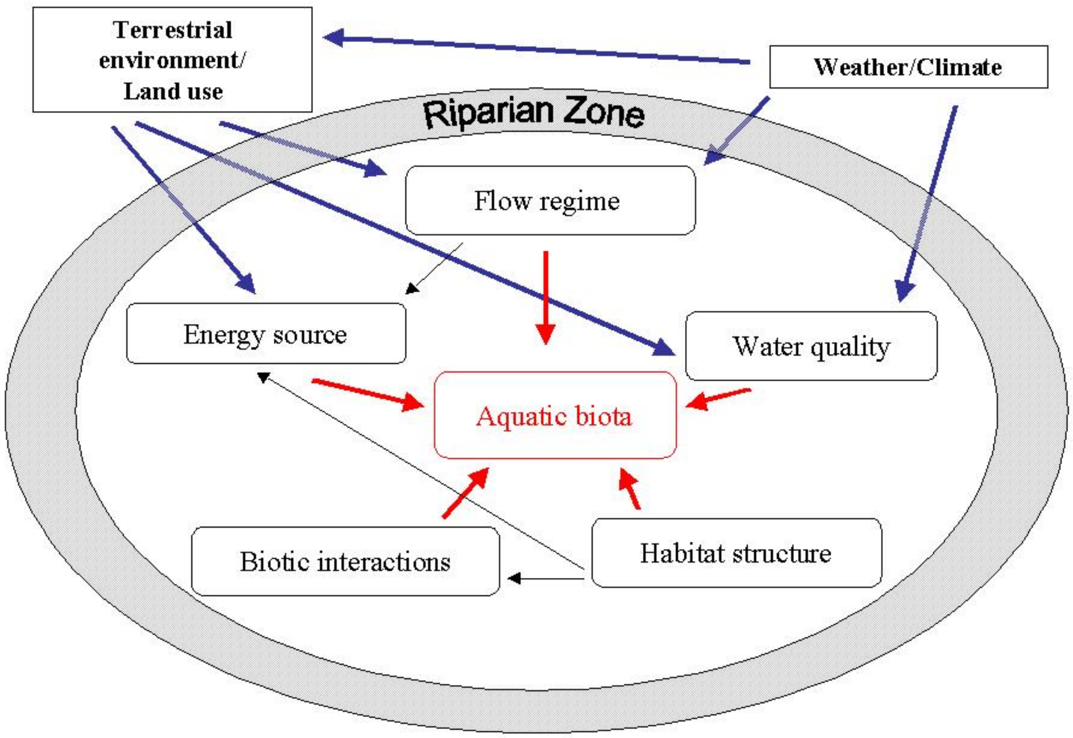

Figure 1. Basic schematic model of a stream ecosystem and its elements (Karr 1991).

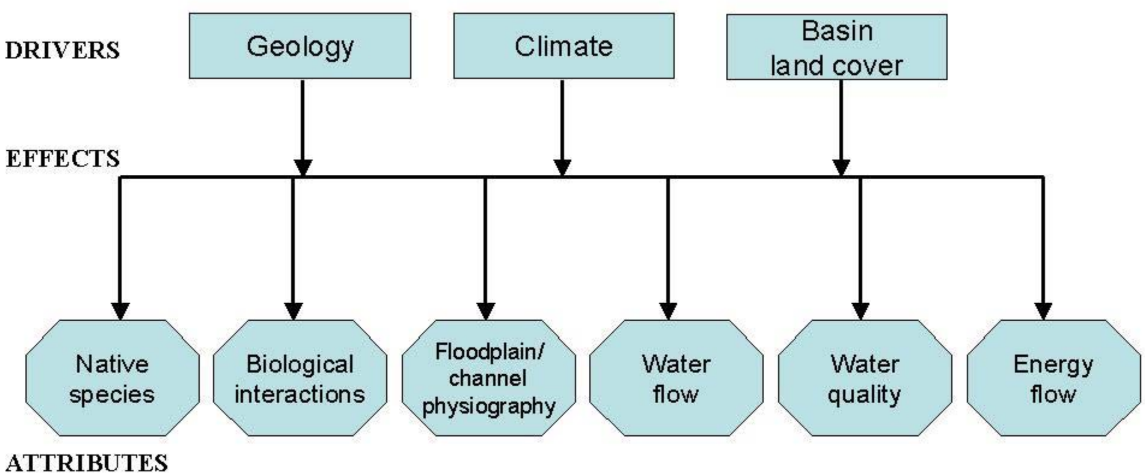

Figure 2. Large river ecosystem conceptual model. Model developed for the NPS Great Lakes Inventory and Monitoring Network of Parks to illustrate basic connections between selected system drivers (rectangles) and attributes (octagons).

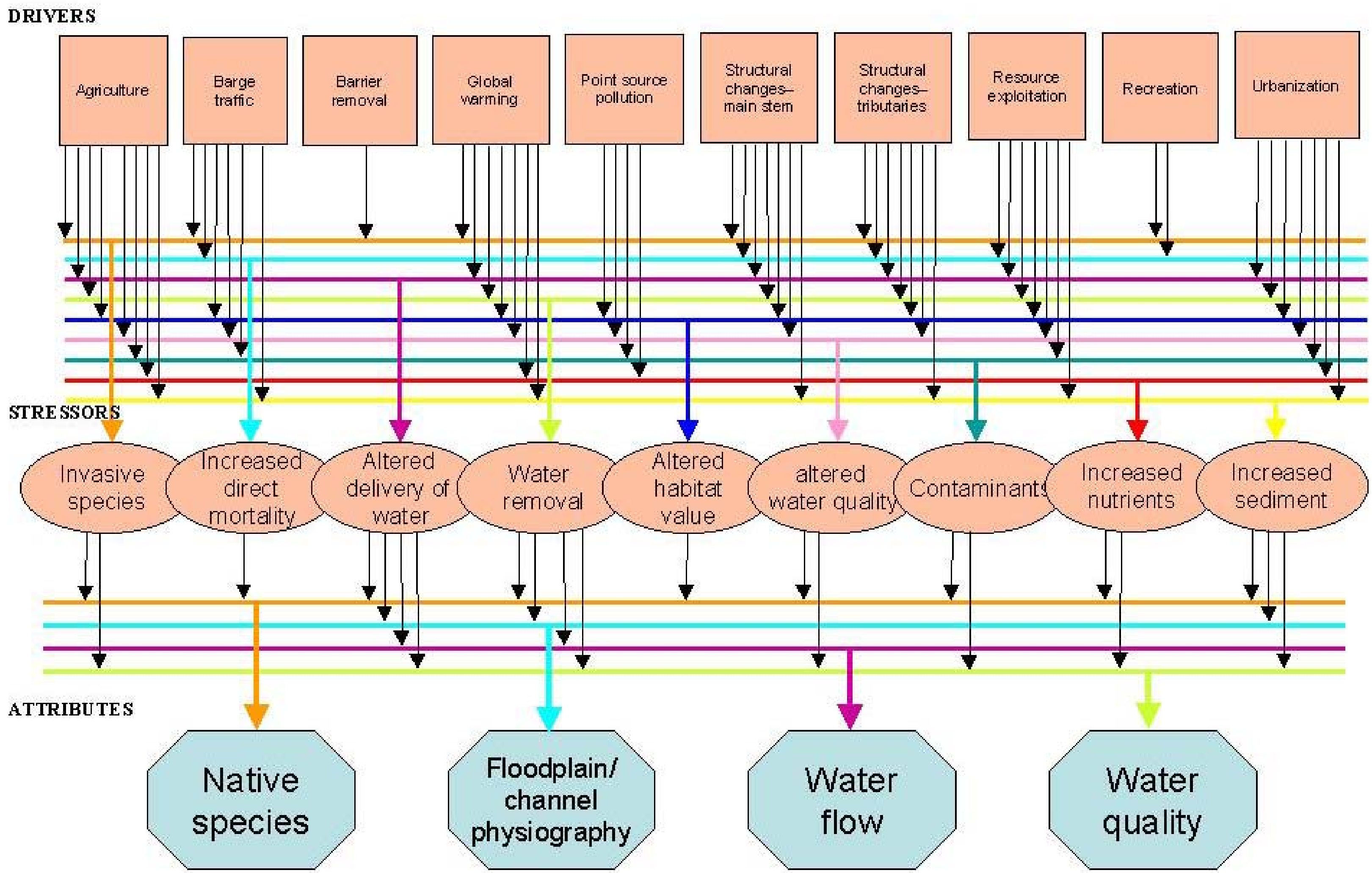

Figure 3. Relationships between anthropogenic drivers, stressors and coarse-level attributes in a large river model. Each stressor (ovals) and attribute (octagons) are represented by thick, colored lines. Connections (probable causal linkages) between drivers (rectangles) and stressors, and between stressors and attributes, are drawn with thin vertical arrows.

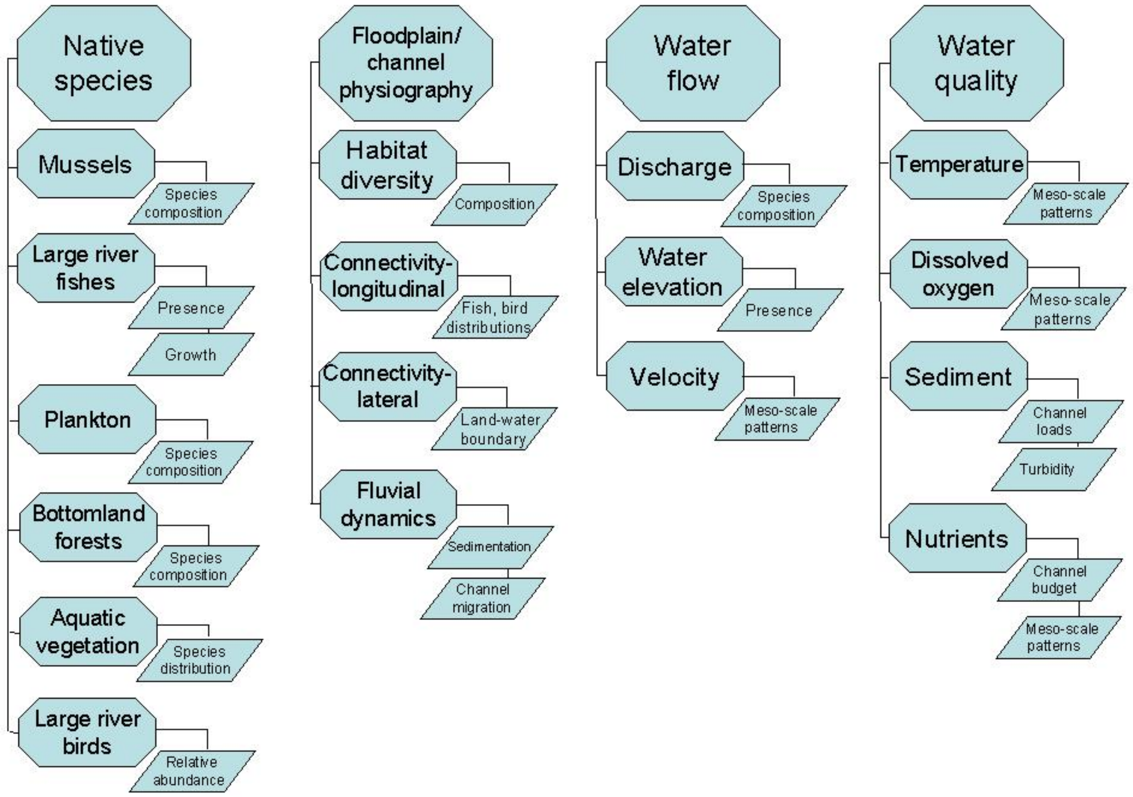

Figure 4. Large river conceptual model relationships between attributes and measures. General attribute categories (larger octagons) are divided into fine-level classes for which specific measures are suggested (parallelograms).

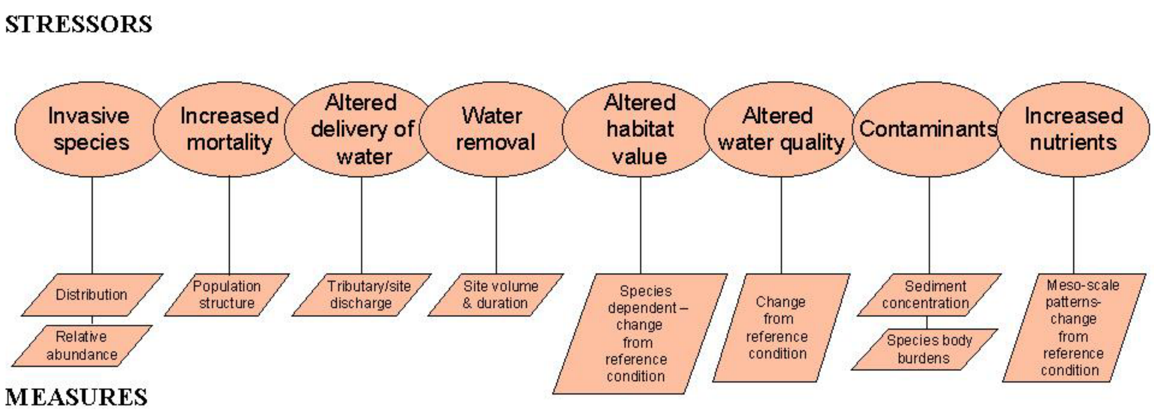

Figure 5. Large river conceptual model relationships between stressors and measures. Direct effects from various stressors (ovals) can be monitored with appropriate measures (parallelograms).

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Great Lakes Conceptual Model

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INTRODUCTION

The National Park System's Great Lakes Network includes units located on two of the Laurentian Great Lakes: Lake Superior and Michigan (the largest and second largest of the Lakes). Despite their large size, these two lakes, as all of the Great Lakes, are sensitive to the effects of physical, chemical, and biotic stressors. Concern over the deterioration of water quality and changes to the fisheries of this system has led to the "Great Lakes Water Quality Agreements" first established in 1972. These agreements and various remedial actions, and monitoring programs have led to improvements in the water quality of the Great Lakes system. The Great Lakes Water Quality Agreement takes a broad, systemic view of the interaction among physical, chemical, and biological components in the Great Lakes Basin. In 1987, the Agreement was revised to strengthen management provisions, call for development of ecosystem objectives and indicators, and address nonpoint sources of pollution, contaminated sediment, airborne toxic substances, and pollution from contaminated groundwater.

The emphasis of this conceptual model (Figure 1) is on the nearshore littoral habitats of the Great Lakes that form the interface between the deep open waters and upland shoreline. This habitat is underlain by Precambrian rocks in Lake Superior that form much of its shoreline. In contrast, softer Paleozoic rocks including limestone, dolomites, shales, and sandstones underlie much of Lake Michigan. Despite these physiographic differences, nearshore littoral habitats are subjected to a similar set of diverse impacts. The major threats to the nearshore habitat include indirect effects of watershed development, changes in physical processes, point and non-point pollution, and introduction and presence of exotic species.

These stressors affect the ecological condition of this habitat, leading to ecological change. Land use change can result in increased hydraulic, sediment, nutrient, and contaminant loadings to the nearshore. Predicted climate scenarios will result in changes in temperature affecting physical, chemical, and biological processes in these habitats. Organic chemicals and heavy metals pose significant risks for benthic invertebrates, fish populations, colonial nesting water birds, and fish-eating mammals that utilize nearshore habitats. The ecological effects of exotic species in the Great Lakes, including sea lamprey (*Petromyzon marinus*), white perch (*Morone americana*), ruffe (*Gymnocephalus cernuus*), zebra mussel (*Dreissena polymorpha*), and the spiny water flea (*Bythotrephes cederstroemi*), continue to be serious and in many cases problematic.

The SOLEC process (State of the Lakes Ecosystem Conferences 1994, 1998, 2000, 2002) has identified a large number of indicators for potential use in assessing the integrity of the nearshore waters of the Great Lakes. These indicators measure response to a variety of stressors (identified above) and serve as indicators of ecosystem condition. However, the nearshore ecosystem responds to the synergistic effects of these multiple stressors in complex ways and at a variety of spatial and temporal scales.

Nearshore habitats

The nearshore habitat has been defined as the open water area of the lake to a depth of 80 meters. For purposes of this model, it is defined as the nearshore open water area to a depth of 20 meters that includes the littoral zone and the shallow bottom slope from the shoreline. Embayments are nearshore areas that are connected to Lake Superior but are partially protected from the physical dynamics that occur in the nearshore open water. Embayments include bays, harbors, and estuaries and often have unique physical properties setting themselves apart from the rest of the nearshore.

A defining feature of the nearshore habitat is the presence of a temperature dependent phenomena characteristic of large lake systems - the thermal bar. The thermal bar forms because the large mass of deep offshore waters warm more slowly than nearshore waters in the spring, resulting in a density difference between these two water masses and the formation of a vertical cold water - warm water interface that prevents mixing of the nearshore and deep colder waters of the open lake. The thermal bar may persist through June in Lake Michigan-Huron and longer on Lake Superior. However, eventually the entire surface warms and the lake becomes thermally stratified.

ECOSYSTEM DRIVERS AND STRESSORS

Physical Processes

The Great Lakes, especially Lake Superior, have been slowly warming over the past 100 years. Changes in future climate are also likely to result in larger variations in lake level, ranging anywhere from 0.3 to 8.1 meters (Kling 2003), leading to changes in biogeochemical cycling of nutrients, including phosphorus, as well as metals and contaminants. Changes in surface water temperatures due to climate change that exceed 2° to 5°C may affect the distribution of cold-water fish, replacing herring, trout, and steelhead with warm water species like perch and walleye (Kling 2003).

Lenters (2001) analyzed long-term trends in the rate of change in monthly mean Great Lakes water levels from 1860-1998. He documented important changes in the seasonal cycle of Great Lakes water levels. Some of the changes that were detected are consistent with the predicted impacts of global warming but responses to seasonal changes in precipitation and/or changes in land use cannot be ruled out.

Trebitz et al. (2002) examined the relative roles of tributary flows and lake connections influencing the structure and function of Great Lakes coastal wetlands and embayments. They concluded that an understanding of these flows and landscape setting is important in examining the response of embayments to anthropogenic stressors.

Increased sediment loading can affect coastal ecosystems by a reduction of light penetration leading to decreases in food sources (phytoplankton) for fish, crustaceans, and other organisms, and by settling and covering critical benthic habitats, burying fish spawning areas, and degrading water quality. Long-term trends in sediment runoff from coastal watersheds in Lakes Michigan and Superior have been summarized by Robertson (1997). Robertson calculated loads of suspended sediment and total phosphorus from 1975-1990 for 18 tributaries. Long-term suspended sediment loads were affected primarily by the topography of the region and secondarily by texture of the surficial sediments. On the other hand, average total phosphorus loads were affected primarily by sediment texture and secondarily by land use type in the adjacent catchment.

Climate and geologic setting may both play important roles in sedimentation rates. Johnson and Johnston (1995) found that north and northwest facing shores in the western arm of Lake Superior eroded significantly faster than south facing shores of the same sediment type due to major storm winds and waves approaching from the northeast. More easily erodible red clay bluffs and northern exposure make the Wisconsin shore of the western arm a major sediment source (Kemp et al. 1978).

Human Impacts

Land use change is a complex process that results from human activities in the surrounding watershed and can lead to significant changes in flows to receiving waters. Detenbeck et al. (2003) examined the impacts of hydrogeomorphic region, catchment storage, and forest cover on base flow and stream water quality flowing into Lake Superior. Water quality was affected by a combination of regional influences, catchment storage, and mature forest cover.

Changes in these flows and the amount of sediment, nutrients, or contaminants result in shifts in macroinvertebrate, plant, and fish communities and changes in population abundance. The thermal bar - a vertical front where warm and colder waters meet- acts to constrain this runoff from the upland in the nearshore waters during the spring and early summer, exacerbating these effects. Prior to the 1970s excessive nutrient loads led to deterioration of the benthic environment and declines in sensitive species (Cook and Johnson 1974). However, densities of major macroinvertebrate groups changed dramatically at sites shallower than 50 meters in southern Lake Michigan between 1980 and 1993 as a consequence of reductions in phosphorus inputs to the lake and the expansion of exotic zebra mussel populations.

Changes in the phytoplankton community of aquatic systems have been closely linked to disturbances from nutrients, salinity, sediments, and acidification (Dixit et al. 1999). Nutrient loading (particularly phosphorus) from tributaries and point sources in the Great Lakes has caused eutrophication in bays and nearshore waters. Shifts in plankton abundance and community composition in Great Lakes coastal waters have been recorded in examinations of long-term data sets (Makarewicz and Bertram 1991). Kerfoot (unpublished data) suggests that the coastal waters of Lake Superior, in the vicinity of the Keweenaw Peninsula, seem to be undergoing “progressive eutrophication” with the waters becoming more productive and showing a change to warmer water species. Phosphorus also seems to be implicated and the thermal barrier apparently concentrates phosphorus near the shore region.

The presence of organic chemical contaminants and heavy metals in the Great Lakes food web is widely recognized and studied (Canfield et al. 1996, Cook et al. 1997, and Kubiak et al. 1989). Adverse effects in birds (e.g., egg-shell thinning) and fish (e.g., tumors) are well documented (Ryckman et al. 1998, Scheider et al. 1998). Organochlorine compounds are persistent and can accumulate in the aquatic food chain at sublethal concentrations, often resulting in impaired reproduction (Mac and Edsall 1991) and impairment of the immune system. Rowan and Rasmussen (1992) showed that concentrations of persistent organochlorines in sediment and water cannot alone explain the between-lake variability in fish contaminant concentrations. The other important factors include: fish lipid content, trophic position, and trophic structure of the food chain. Exposures to contaminants that bioaccumulate pose a great risk to higher trophic levels of the food chain.

Atmospheric deposition is an important pathway for the transport and distribution of PCBs (Swain 1978) and other organochlorine products (Andren 1988). Triazine herbicides are being transported atmospherically for hundreds of kilometers and being deposited by precipitation across the Great Lakes (Thurman and Cromwell 2000). Atmospheric sources of mercury range from 50 percent of the total flux in Lake Michigan to 38 percent for Lake Superior (Rossman 1999).

Researchers have noted a class of chlorinated chemical compounds that disrupt normal endocrine functions in fish and wildlife (Ankley and Giesy 1998). The widespread use of synthetic estrogens in birth control pills and hormone replacement therapies is another source of endocrine disrupters, as are cosmetics, cleaning products, and pesticides. There is now strong evidence that environmental estrogens cause reproductive impairment including sex differentiation, sexual development, and sexual dimorphism (Ankley and Giesy 1998). Two- to four-year-old salmon in the Great Lakes have been found to have enlarged thyroid glands. Precocious sexual maturity, poor egg survival, and low thyroid content in eggs are also common (Colburn et al. 1993).

Biotic Impacts

Invasion by nonindigenous species is an ongoing process in the Great Lakes with largely unknown consequences but potentially major ecological implications. The abundance and species composition of the prey and young predator fish populations in the Great Lakes are affected by invasive species. Kolar et al. (2002) experimentally examined the interactions among zebra mussels, invertebrates, and European ruffe and yellow perch. They concluded that the effects of predation between and among native and nonindigenous species may have profound effects on the composition and structure of the nearshore communities of the Great Lakes. Kitchell et al. (2000) discussed the differences between higher turnover rate exotic rainbow smelt and its primary predators (exotic Pacific salmonids) and the slower turnover rates that occur among native lake trout and burbot and their prey (herring, smelt, cisco, and sculpins) in Lake Superior. The abundance of forage fish is a key constraint for all salmonids in Lake Superior.

The introduction of sea-lamprey, rainbow smelt, ruffe, round goby, spiny water flea, and other exotic aquatic species in Lake Superior has resulted in a diverse food web with largely unknown species interactions compared to the more simple food webs found earlier.

Zebra mussels (*Dreissena polymorpha)* are invasive filter feeders found in shallow coastal waters that quickly colonize hard surfaces and soft sediments. They also encrust native mussels, leading to declines in their number. They filter phytoplankton and small zooplankton that serve as food for forage fish, thereby potentially altering food web dynamics. Fahnenstiel et al. (1995) studied zebra mussel invasion in Saginaw Bay on Lake Huron. They found that decreases in phytoplankton productivity in the inner Bay after zebra mussel invasion were compensated by increases in benthic production. However the shift from a pelagic to a benthic dominated system will have long-term effects on food web structure of this system. Zebra mussel invasions in Lake Michigan have also been correlated with serious declines in *Diporeia* populations. *Diporeia* is a major link between pelagic production and fish in the Lake Michigan food web (Gardner et al. 1990).

The European ruffe (*Gymnocephalus cernuus*), a non-native perch species, was introduced into Lake Superior in the 1980s in ballast water discharged from vessels. Ruffe grow in a wide range of temperatures including shallow, warm, nearshore habitats with eutrophic conditions where they may disrupt nearshore food webs (Ogle et al. 1995). Walleye, perch, and smaller forage fish with similar diets and feeding habitats may be affected by increases in ruffe populations.

The round goby (*Neogobius melanostomos*) is an aggressive fish that appeared in the Great Lakes in the 1990s. This benthic fish species prefers rocky or gravel areas in nearshore habitats. Round gobies eat the eggs and fry of native benthic fish, including sculpins and darters, and displace other fish species from rock habitats that they use for spawning (French and Jude 2001). They, like the ruffe, are capable of surviving in areas with degraded water quality. Gobies are themselves preyed on by yellow perch, walleyes, and brown trout. But because they include zebra mussels (a filter feeder) in their diet, they may act to transport contaminants directly to sport fish.

The spiny waterflea (*Bythotrephes cederstromei*) is representative of a group of exotic zooplankton invading the Great Lakes. The spiny waterflea eats smaller zooplankton and so competes directly with juvenile fish for food. At the same time, the presence of large spines on their bodies is a protection from predation by smaller forage fish.

The abundance and species composition of Great Lakes fish assemblages have been greatly influenced by overfishing, establishment of exotic species, predator stocking programs, and habitat destruction. Regier and Loftus (1972) and Lawrie and Rahrer (1972) documented the effects of over-exploitation of salmonid communities in the upper Great Lakes. The effects of over-exploitation coupled with introduction of the sea lamprey lead to the collapse of these fisheries. However, sea lamprey control and stocking has led to successful restoration of the native lake trout populations (Kitchell et al. 2000).

ECOSYSTEM ATTRIBUTES AND MEASURES

The development of indicators of biological and ecological condition, and interpretation of those responses using measures of exposure to stress, has been a focus of research in the Great Lakes and forms the basis for evaluations of the ecological integrity of the Great Lakes. The Great Lakes Water Quality Agreement of 1987 called for the development of biological measures of ecosystem integrity. The SOLEC process has identified a number of indicators to assess the integrity of the Great Lakes (Bertram and Stadler-Salt 1999), but these have not been adequately evaluated or tested nor have they been specifically developed for the nearshore environment. The SOLEC process has emphasized four categories of stressors: non-native species, toxic contaminants, excessive nutrients, and physical processes. The list of indicators that have been derived through the consensus process used by SOLEC includes, among others: contaminant concentrations in the water, sediments, and tissues of higher trophic level species and bird eggs, and the presence of physical deformities; presence and abundance of key benthic organisms (e.g., *Hexagenia spp*., *Diporeia spp*. and unionid mussels); plankton community diversity and species abundance; patterns of abundance of prey fish populations; and levels of *E. coli* and fecal coliform in nearshore waters.

Others have attempted to develop indicators appropriate for assessing the ecological integrity of Great Lakes freshwater wetlands (Burton et al. 1999, Wilcox et al. 2002). They examined a suite of biological and physical candidate indicators. Plant, fish, and invertebrate indicators studied in Lake Superior and Lake Michigan-Huron coastal wetlands (Wilcox et al. 2002) were inconsistent in their ability sort sites along gradients of disturbance. Burton et al. (1999) used invertebrate data to compare Lake Huron coastal wetlands between categories of anthropogenic disturbance. A preliminary Index of Biotic Integrity (Karr 1991) seemed to provide an accurate depiction of wetland integrity but was not recommended as a definitive assessment tool.

Indicators are variables that are so closely related to certain ecosystem functions that their presence or value is evidence of the existence of specific functions or how well those functions are being performed. Indicators measure characteristics of the environment that can provide quantitative information on ecological integrity. To be used in a long-term monitoring program, indicator variables must demonstrate predictable relationships with ecosystem condition. Careful selection of indicators is required to ensure adequate sensitivity to stress and disturbance. At the same time, the response to stressors must also be distinguishable from the natural variability exhibited by the indicator. Therefore, it is important to know the relationship between ecosystem characteristics, the sensitivity to stress and disturbance, and the natural temporal and spatial variability when choosing among various potential indicators for inclusion in a monitoring program. Finally, important components of indicator development should include applicability to a properly classified group of sites such that the diversity and composition of the assemblages within the group is minimized. In addition, the reference, or baseline, condition must be defined properly.

The development of indicators for the nearshore environment of Lakes Michigan and Superior can draw upon the efforts of the various groups involved in the development of indicators for the Great Lakes, but the challenge is to select those indicators appropriate for the nearshore environments of the units in the National Park system.

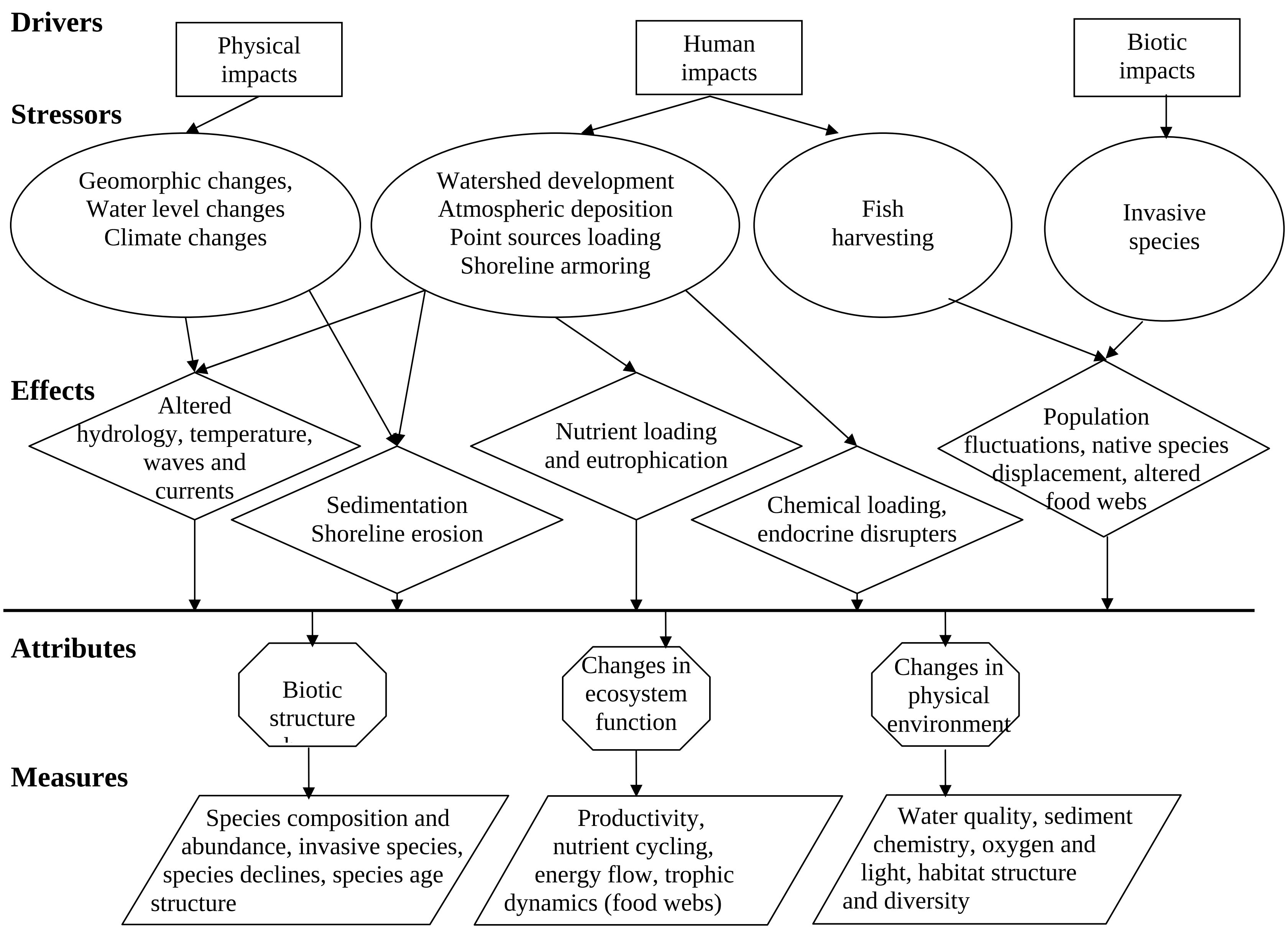

Figure 1. Conceptual model of the nearshore environment of the Great Lakes. Model developed for the NPS Great Lakes Inventory and Monitoring Network of Parks to illustrate connections between drivers and ecosystem attributes.

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